THE INFLUENCE OF FLOW ALTERATION ON INSTREAM HABITAT AND FISH ASSEMBLAGES

By

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Abstract: Globally, the instream habitat and biotic community of riverine systems are declining. The primary threat to rivers is flow regime alteration through dams, landscape alteration, and climate change. The natural flow regime is the natural pattern of a rivers flow. The flow regime is vital for maintaining abiotic and biotic stream components, including the thermal regime of rivers (i.e., average, maximum and minimum temperature). Increased stream temperature can influence species direct and indirect survival, as well as many life history events. The objectives of my Master's research were to 1) develop flow-ecology relationships for stream habitat and fishes from the Arbuckle Mountain and Ozark Highland ecoregion and 2) determine the maximum thermal tolerance of stream fishes from the Arbuckle Mountains. Flow-ecology relationships were determined through the development of linear models for both stream habitat (i.e., deposited sediment, channel-unit diversity, residual-pool depth, and bankfull width-to-depth ratio) and fish assemblages (i.e., coarse-scale reproductive guilds and finer-scale reproductive-taxonomy guilds) to determine their relationship with flow alteration. These flow-ecology models showed that many stream abiotic and biotic characteristics were positively influenced by dynamic flow conditions, such as, increased magnitude and number of reversals. For example, stream fish diversity and reproductive guild diversity were positively influenced by increased maximum flows. Abiotic and biotic flow-ecology relationships can further improve the development of environmental-flow standards. I also determined the critical thermal maxima (CTM) of 15 species and the longer-term tolerance of 10 fish species from the Arbuckle Mountains. Longer-term studies had both a spring-fed and non spring-fed treatment that mimicked the thermal regime of Arbuckle Mountain streams. Comparing the results of the CTM and the longer-term study improves our understanding of species thermal tolerance and acclimation ability. Results showed that pelagic species had higher thermal tolerances than benthic species and had greater acclimation ability. Results from both objectives provide insight on the susceptibility of species to future flow and thermal alterations. This can be used to predict future fish assemblage changes and determine species of conservation concern.

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CHAPTER I

INTRODUCTION

Lotic fishes are declining at a concerning rate due to changes in the abiotic structure of streams. Globally, rivers are among the most imperiled ecosystems and, as human populations continue to increase, so does the pressure on this limited resource (Tharme 2003). Jelks et al. (2008) estimated that 39% of the freshwater fishes in North America are imperiled due to flow alteration, invasive species, habitat fragmentation, and habitat degradation. Deforestation for agriculture is the most widespread landscape alteration in North America and it has drastic effects on river habitat, biodiversity and water quality (Allan 2004). However, the greatest threat to riverine systems is the storage of water via dams and reservoirs. Tharme (2003) stated that only 2% of the rivers in the United States are still free flowing and unaffected by dams. Although dams are the main source of flow alteration, the flow regime is also being altered via groundwater pumping (Fitzhugh and Richter 2004; Acreman et al. 2008), riparian vegetation removal (Allan 2004), and climate change (Caissie 2006). Flow alteration is the primary factor influencing the loss of fish-species biodiversity and abundance (Poff et al. 1997; Bunn and Arthington 2002).

The flow regime in streams can be characterized using the average, the extremes (i.e., low and high flows), and the variability of discharge events. These characteristics can be used to describe the five main components of the flow regime: timing, magnitude, duration, frequency, and rate of change (Poff et al. 1997). Briefly, these flow components are defined as: timing, the seasonality or predictability of certain flow events; magnitude, the amount of water moving through the river at a given time; duration, the length of time that flow events occur for; frequency, the number of times those flow events occur within a given time frame; rate of change, the length of time it takes flow events to change in magnitude. Interactions between the flow regime and the associated landscape determines stream structure, including channel shape and size, channel-unit composition, substrate composition (Bunn and Arthington 2002), floodplain connectivity (King et al. 2003; Acreman and Dunbar 2004), and sediment-transport rates (Allan 2004). Fishes have evolved to exploit the various instream structures maintained by the flow regime and life-history events often correspond with different flow components (i.e., high or low-flow events).

Native fishes have adapted to the natural flow regime and rely on specific flows at certain times of the year to complete life-history events (e.g., migration, spawning, and egg hatching; Poff et al. 1997). Potamodromous migrations by freshwater fishes, including diminutive fishes such as the Pecos Bluntnose Shiner *Notropis simus*, are thought to be necessary for recolonization and to allow drift distances for offspring (Chase et al. 2015). High-flow events can prevent the establishment of invasive species, while creating optimal spawning conditions for native fishes (Marchetti and Moyle 2001). For example, species within the lithophil reproductive guild (i.e., fish that deposit

eggs on clean gravel and cobble substrate), such as the Slenderhead Darter *Percina phoxocephala,* spawn in conjunction with high flows because of the increased oxygen and reduced sediment surrounding the substrate (Brewer et al. 2006). Other species, including the federally threatened Arkansas River Shiner *Notropis girardi*, have a reproductive peak associated with high water (Durham and Wilde 2009) and need continuous flows to allow for the subsequent drift and development of their eggs and larvae (Perkin and Gido 2011). Disruption of natural-flow patterns is thought to be a primary factor related to the decline of Arkansas River Shiner and several other members of the pelagic broadcast spawning guild of fishes within the Great Plains (Worthington et al, unpublished). In fact, at least 13 species within the pelagophil reproductive guild are listed as some form of conservation concern (Warren et al. 2000; Jelks et al. 2008). In addition to the direct disruption of life histories, altered flows can result in the homogenization of stream habitats (i.e., lack of flows that maintain complexity) and subsequent reductions in overall stream-fish diversity (Moyle and Mount 2007).

Changing flow patterns may alter many physicochemical conditions of streams. For example, the Missouri River below Fort Peck Dam has an altered flow regime (e.g., reduced high-flow events, and increased baseflow), which led to an altered sediment regime and streambed aggregation (Bowen et al. 2003). Also reduced mesohabitats, wider channels and a reduction in the abundance of submerged macrophytes were related to reduced magnitude and altered timing of seasonal flows in the Segura River Basin, Spain (Belmar et al. 2013). Reduced discharge can influence the width-to-depth ratio of rivers, subsequently decreasing available habitat and biodiversity (Dewson et al. 2007). Reductions in groundwater inflows due to pumping can reduce the amount of nutrients

entering the stream channel (Dahm et al. 2003). Reduced baseflows, from either groundwater or surface water withdrawals, can increase daily maximum temperatures and alter seasonal temperature fluctuations (Cazaubon and Giudicelli 1999; Risely et al. 2010). Stream temperature increases could reduce dissolved oxygen concentrations and reduce fish survival by exceeding their thermal limits (Morrill et al. 2005).

Atmospheric temperature and precipitation patterns are expected to change due to climate and other landscape changes, thus affecting instream temperature regimes. Shading, the temperature of incoming water (e.g., precipitation, surface runoff, and groundwater), and heat exchange at the air-water interface are factors that control stream-water temperatures (Morrill et al. 2005). Reductions in baseflow and riparian vegetation increase the amount of solar radiation entering streams, causing increased maximum temperature and greater diel temperature fluctuations (Allan 2004; Whitledge et al. 2006; Mayer 2012). Globally, atmospheric temperature has increased over 1°C in the last century and is expected to increase 1 – 3°C in the next century (Morrill et al. 2005). These predicted increases in air temperature are expected to increase stream temperatures in the southeastern U.S. by 2 – 3°C in the next 50 years (Van Vliet et al. 2013). Temporal variability of natural thermal regimes (e.g., diel fluctuations, cumulative degree days, maximum and minimum temperatures) is important to maintain ecological stream processes (Maheu et al. 2015). Streams with altered flows will be more susceptible to increases in temperature from climate change (Morrill et al. 2005; Kundzewicz et al. 2008; Van Vliet et al. 2013). Like altered flow regimes, changes in instream thermal patterns have the potential to disrupt the life history of fishes.

Anticipated increases in stream temperatures could be uniquely problematic for stream fishes due to the dispersal limitations of many species. Alteration to the thermal regime could cause stream temperatures to exceed the maximum-thermal tolerance of stream fishes (Matthews and Zimmerman 1990). In order for species to persist with increases in stream temperature, they must either adapt or disperse to a region with a more tolerable temperature (Matthews and Zimmerman 1990). The ability for many species to disperse to areas of thermal refuge is limited by habitat fragmentation (e.g., damming and road crossings) (Fitzhugh and Richter 2004) and the unsuitable physicochemical character of different streams (e.g., changes from lowland to higher elevation streams). Also, east to west flowing streams, common in the Great Plains, prevents fish from dispersing to cooler temperatures in the north (Matthews and Zimmerman 1990). The paucity of thermal tolerance information for many stream fishes makes it exceptionally difficult to predict the effects of increased temperatures on fishes.

Because changes in flow regimes and instream temperatures are intertwined in many respects, understanding how each affects the persistence of fish populations would be beneficial to the conservation and management of streams. In order to make adequate predictions about the effects of flow and thermal regime changes on fishes, we need to know three things. First, we need a better understanding of how altered flow regimes affect the persistence of different groups of fishes at a broad-spatial scale (see Poff et al. 2010). Next, we need to understand the thermal tolerances of stream fishes to predict which fishes will be most susceptible to associated thermal changes to streams. To make our conclusions more general, an examination of how thermal tolerances change across stream types would be beneficial to integrate into current classification schemes

associated with environmental flow planning across broad scales (e.g., ELOHA, Poff et al. 2010). Finally, coarse-scale modeling that can integrate flow and temperature changes across a landscape while integrating fragmentation barriers would aid management in prioritizing stream reaches that would most benefit from environmental-flow designations. The goal of this project is to address the first two information needs and provide the necessary information for follow up via more coarse-scale assessments. My specific objectives are to determine the relationship between different levels of flow alterations on the fish assemblage and lotic habitat in the Arbuckle Mountain and Ozark Highland ecoregions, and to determine the critical thermal maxima (CTM) of 15 fish species and determine the longer-term temperature tolerance of 10 species under varying thermal regimes from the Arbuckle Mountain Ecoregion.

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CHAPTER II

INFLUENCE OF FLOW REGIME ALTERATIONS ON FISH ASSEMBLAGES AND THE ABIOTIC STRUCTURE OF STREAMS

ABSTRACT

The natural flow regime of streams maintains complex instream habitat and supports native fish diversity. Globally, the flow regime is being altered and biotic relationships with flow components that support broad environmental-flow standards are lacking. The objective of my research was to develop flow-ecology relationships for stream habitat and fishes. Habitat characteristics (i.e., bankfull width-to-depth, residual pool depth, channel-unit diversity, and deposited sediment) and the fish assemblage was sampled in 14 streams of the Arbuckle Mountain and Ozark Highland ecoregions. Fish flow-ecology relationships were developed for coarse-scale reproductive guilds and finer-scale-taxonomic-guild subsets. Ordinary least squares and generalized linear models were used to determine the relationship between 10 flow variables and habitat and fish guilds. Many flow-ecology relationships were best described using flow magnitude. Flow magnitude was positively related to stream-fish diversity. Reproductive guild relationships were often driven by the most common species' within the guild. For example, the abundance of 14 species of lithophil minnows, like the broader lithophil guild, was negatively

related to low-pulse duration. However, several other taxonomic subsets showed opposite relationships to flow metrics that were significant for the broader guild. For example, lithophilic darters abundance increased as the number of flow reversals increased and the lithophilic sucker abundance increased as high-pulse frequencies increased. Other flow-ecology relationships were also dependent on other dynamic flow variables (i.e., high-pulse frequency, and reversals). Further, finer taxonomic groups showed similar relationships with flow metrics that were also significantly related to abiotic parameters such as sedimentation. Results from this study are useful for the development of instream monitoring programs and for developing broad scale environmental-flow standards in groundwater-dominated systems.

INTRODUCTION

Alteration of long-term annual and seasonal flow patterns or flow regime is causing significant changes to the structure and function of rivers. Carlisle et al. (2011) determined that flow magnitude (i.e., the amount of water at a given point in time) is altered in most rivers in the United States. Magnitude and other parameters that describe a river's flow regime (frequency, timing, duration, and rate of change; Poff et al. 1997) affect the quality and availability of instream habitat, which subsequently relates to declines in fish biodiversity and abundance (Orth 1987). Regulation via dams and off-site water storage homogenizes downstream river flow and often relates to an increase in habitat generalists and invasive species (Poff et al. 2007; Döll et al. 2009). Impoundments capture peak flows in spring and either slowly release excess water (i.e., above normal pool) over summer (reducing magnitude and extending flow duration, Magilligan and Nislow 2005) or release no water at all (Palmer et al. 2009). Loss of spring peak flows

relates to wider and shallower stream channels due to altered sediment dynamics (Tyus 1990). Further, reduction in high-discharge events reduces overall habitat heterogeneity, flushing of fine sediments, recruitment of large woody debris, and floodplain connectivity (Poff et al. 1997; Crook and Robertson 1999; Craven et al. 2010). These changes have negative consequences for stream fishes. For example, Smallmouth Bass *Micropterus dolomieu* abundance is reduced when stream reaches comprise a large proportion of pool habitat even though this is the primary habitat used by this species (Sowa and Rabeni 1995; Brewer 2013). Excess deposited sediment can influence successful fish ontogeny by altering oxygenation of eggs (Jennings et al. 2010), reducing suitable habitat for multiple life stages (larva, Jensen et al. 2009; juveniles, Suttle et al. 2004, adults, Berkman and Rabeni 1987; spawning adults, Tyus 1990), and reducing forage availability (Henley et al. 2000). The successful ontogeny of fishes has evolved around specific habitats that are maintained by natural flows, although groups of fishes that share similar traits may respond to flow changes similarly.

Fishes may be grouped to reflect similar responses to environmental perturbations. For example, fishes rely on specific flow components (e.g., floods, medium and low flows) at certain times of the year to complete life-history events (e.g., migration, spawning, and egg hatching; Starrett 1951; Larimore et al. 1959; Moyle and Li 1979; Grossman et al. 1982; Schlosser and Toth 1984; Schlosser 1985; Cowx et al. 2012). Collectively, native fishes in North America have generally adapted to natural summer low flows, which reduce available habitat and increase competition, helping prevent non-native species invasions (Tharme and King1998; King et al. 2000; Acreman and Dunbar 2004). Taxonomically-related species, or species that use resources similarly,

may respond likewise to flow alteration. Balon (1975) categorized reproductive guilds by grouping species together that were thought to require similar stream characteristics for successful spawning. Guilds are useful for examining responses to perturbations without proceeding on a species-by-species basis. For example, many pelagophil fishes (i.e., broadcast-spawning fishes that require moving water during early ontogeny; Worthington et al. 2014) are declining due to similar responses to fragmentation and flow alteration (Gido et al. 2010). In fact, 13 of 20 species in this reproductive guild of the Great Plains are listed in some form of conservation concern category and there are limited data on the remaining seven species (Worthington et al., unpublished). Carlisle et al. (2011) found that lithophilic species (i.e., spawn on substrate and do not circulate water around eggs; Balon 1975) were more susceptible to reductions in flow magnitude. Unfortunately, little research has focused on the relationship between guilds or groups of species and flow alteration, thereby preventing advances in environmental-flow science (Craven et al. 2010; Poff et al. 2010).

Ecologists have made substantial advancements developing environmental-flow approaches that move from single river flow designations to regional planning (see McManamay et al. unpublished); however, our understandings of abiotic and biotic relationships that support these broader efforts have lagged behind. Since the 1940's, ecologist have been studying instream flows focusing on defining minimum flows (Arthington et al. 2006). Initial standards, based solely on minimum flows, were not successful at maintaining flow regime variation or providing necessary flows for native species (Richter et al. 1996; Poff et al. 1997; Lytle and Poff 2004). In the last 20 years, mimicking and developing flow standards based on the natural flow regime has become

the accepted method for improving habitat and fish assemblages in regulated rivers (Poff et al. 2010; Kiernan et al. 2012; Richter et al. 2012). Although many ecologists have proposed flow standards for single rivers based on natural flow regimes (e.g., Freeman et al. 2001; Marchetti and Moyle 2001; Kiernan et al. 2012), few studies have shown how coarse-scale fish assemblages respond to flow alterations (Poff and Zimmerman 2010). For example, Kiernan et al. (2012) showed increases in native fish abundance and diversity coupled with decreases in invasive species abundance downstream of a California dam after implementation of flow standards mimicking natural flows. The Ecological Limits of Hydrologic Alteration (ELOHA) is currently the most commonly-used method for determining flow-ecology relationships for groups of rivers based on their level of flow alteration and influences on the fish assemblage (McManamay et al. 2013). Although the ELOHA framework is well accepted, data supporting flow-ecology relationships for groups of fishes and habitat characteristics are lacking to support these frameworks.

The importance of the flow regime to native fishes is widely accepted by ecologists, but few studies demonstrate which flow parameters are most important for species or guilds and how they are affected by different levels of alteration (Arthington and Pusey 2003; Poff et al. 2010). A literature review by Poff and Zimmerman (2010) found that most flow-ecology studies focused only on flow magnitude. Recently, some studies have identified the relationship between flow parameters and certain species (e.g., Bice et al. 2014; Rolls and Arthington 2014). Although these relationships are helpful, we need to establish more relationships between coarse taxonomic groups or guilds so that

results are comparable across regions and perhaps, more broadly applicable (Freeman and Marcinek 2006; Mims and Olden 2012; McManamay and Frimpong 2015).

Flow standards could be improved by developing flow-ecology relationships that include both biotic and abiotic components of lotic systems. The biotic component has an obvious link to environmental-flow techniques, but predicting abiotic changes could also be useful. Predicting flow alteration across un-sampled stream reaches based on different levels of observed habitat degradation could allow managers to more efficiently predict which fish assemblages are likely to be imperiled. This could be used as a triage approach to target monitoring with limited monetary resources. Further, this could also be useful for starting to separate the influence of direct flow alteration from other catchment-level disturbances (e.g., land use). Therefore, the objectives of this study are to improve broad-scale flow planning by developing flow-ecology relationships focusing on both stream habitat and fish-assemblage changes within reproductive guilds and other similar species groups.

STUDY AREA

Fish assemblage and habitat conditions were sampled in the Arbuckle Mountain and Ozark Highland ecoregions (Figure 1). The Arbuckle Mountains are located in south-central Oklahoma, and the Ozark Highlands are located in northeast Oklahoma, southwest Missouri, and northwest Arkansas. It is hypothesized that prior to the Pleistocene, the topography of these ecoregions was primarily upland and was connected by a historic river (Mayden 1985). During the last interglacial period, the topography between the ecoregions flattened and a stream-capture event separated the regions

(Mayden 1985). The lithology and fish assemblages of the Arbuckle Mountains and Ozark Highlands are still very similar and many fishes (i.e., Least Darter *Etheostoma microperca*, Redspot Chub *Nocomis asper*, Southern Redbelly Dace *Phoxinus erythrogaster*) are endemic to both ecoregions. The hydrology of streams in these ecoregions are similarly classified as stable, high-flow perennial streams, but could be more finely separated based on the amount of groundwater interaction, runoff rate and watershed size (Turton et al. 2009). Streams in the Arbuckle Mountain and Ozark Highland ecoregions are generally clear during baseflows, moderately cool, with stable flows, and typically dominated by coarse substrates (Bart 1989; Seilheimer and Fisher 2008). Most of the streams require spring inflows to maintain the structure, function, and native biota (Seilheimer and Fisher 2008). The Arbuckle-Simpson aquifer supplies water to most of the Arbuckle streams, whereas many aquifers in the Ozark Plateau supply water to the streams of the Ozark Highlands (Bergey et al. 2008). Primary flow alterations in this region are due to dams, ground-water pumping, and landscape alteration from agriculture (Turton et al. 2009).

METHODS

Abiotic variables. Four habitat characteristics (deposited sediment, channel-unit diversity, residual-pool depth, and bankfull width-to-depth ratio) were measured at 11 rivers (Table 1) during summer of 2014 and 2015. The percent deposited sediment (i.e., percent sand and silt ≤ 2mm filling the interstitial spaces of the substrate, Waters 1995) was measured at three haphazardly selected 1-m^2 locations in three runs in each reach (Bain and Stevenson 1999). The approximate area of channel units (riffles, runs, pools, vegetated edgewater and backwater; Rabeni and Jacobson 1993) was measured in each reach (40

times wetted width; Simonson et al. 1994). Channel-unit diversity was calculated using the Shannon-Weiner diversity index as: $H = -\Sigma PlnP$ (P = species proportion; Begon et al. 2006). Residual-pool depth was calculated by subtracting average depths at three riffle crests from deepest depths in associated upstream pools at each study reach (Lisle 1987). I measured bankfull width-to-depth ratio in three haphazardly selected runs in each reach, measured as the channel width at bankfull conditions divided by the average bankfull depth of that cross section (Gordon 2004).

Fish Assemblage. Fish-assemblage data were collected in summer of 2014 and 2015 from 14 rivers of the Arbuckle Mountains, Oklahoma and Ozark Highland, Oklahoma and Missouri). Habitat conditions at three rivers were not measured because of recent rains that caused an influx of woody debris, turbid river conditions, and higher baseflows. Standardized fish-sampling techniques were adapted from Bonar et al. (2009) and are briefly described below. Electofishing was conducted in an upstream direction with tow-barge electrofisher or small (4.27m) boat electrofisher depending on wadeability. Wadeable areas in all rivers were seined in a downstream direction, using a 3.18 mm mesh seine. Five baited (Sudden Impact Team Catfish, Grove) hoop nets and five unbaited hoop nets (four throats with a mesh size of 5.08 cm) were set for 24 h, one net combination (baited and unbaited nets) was set perpendicular to the direction of flow in three pools and two runs (total of 10 nets). Two experimental gill nets (panels with various mesh sizes that were 30 m long) were set in one pool and one run for 24 h. Many fishes were identified and released on site while those difficult to identify (usually small fishes) were preserved in 10% formalin and returned to the lab for later identification. All fishes ≤ 20 mm total length were omitted from the analyses due to difficulties in

identifying very small fishes that were often damaged during sampling. Further, this omitted the few very small fish that were picked up in some of our gears but often not others.

I assigned all species to a reproductive guild (Frimpong and Angermeier 2009) and calculated their abundance and diversity. Lithophilic species spawn on clean gravel and cobble substrate. Phytolithophilic species spawn on clean gravel and cobble as well as aquatic vegetation. Polyphil species build and spawn on substrate nests. Speleophil species spawn in the crevices and pores of the stream channel. Fish-assemblage and reproductive-guild diversity were calculated using the Shannon-Weiner diversity index: $H = -\Sigma PlnP$ (P = species proportion; Begon et al. 2006). Because some portions of guilds may respond differently to flow parameters from others (e.g., benthic darters and pelagic minnows), I broke the four common reproductive guilds into eight taxonomic subsets: 1) lithophil minnows, 2) lithophil darters, 3) lithophil suckers, 4) phytolithophil minnows, 5) phytolithophil darters, 6) polyphil sunfish, 7) and polyphil basses, and 8) speleophil catfish. These eight subgroups were abundant but still diverse within each reproductive guild.

Flow parameters. Flow data were gathered from U.S. Geologic Survey (USGS) stream gage records and analyzed using Indicators of Hydrologic Alteration (IHA; Richter et al. 1996) to determine the 33 flow parameters for all years the gage was active. I calculated a flow-alteration index for each flow parameter as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Where unaltered flows were defined using either the first 15 years the gage was active, if there was no main-stem dam, or the 15 years prior to dam installation if there

was a main-stem dam. The altered flow period was considered the last 15 years the gage was active (2001–2015, Appendix 1). Flow alteration indices represent the percent alteration from the altered to unaltered average flows. Reductions in the magnitude, duration, or other flow regime metrics between unaltered and altered periods resulted in a negative flow index, whereas increases in magnitude or other metrics were indicated by a positive alteration index. No change between the unaltered and altered flows resulted in an index value near zero (i.e., normal flow conditions).

Data Analyses. Multicollinearity can lead to the misidentification of relevant predicator variables (Dormann et al. 2013); therefore, I reduced the number of flow parameters using Pearson's correlation coefficient and professional judgement. Variables were considered collinear when $rho \geq |0.70|$ (Dormann et al. 2013). The choice of which variable to drop was determined first by the variable's ecological relevance to fishes; however, if this was indeterminate, the variable most easily interpreted was retained. I also ensured that at least one flow parameter represented each of the five components of the flow regime (magnitude, duration, frequency, timing and rate of change). Analyses were completed using R Studio version 3.1.1 (RStudio Team 2015).

Ordinary Least Squares (OLS) simple linear regression models were developed to determine the relationship between the uncorrelated flow parameters and the four habitat characteristics. All models were tested for the four assumptions of OLS regression: normality, homoscedasticity, independence and representative of the population (Zuur 2009). All models were ranked using their R^2 values to determine the top models. Top models were selected only if their R^2 were ≥ 0.20, deeming them biologically relevant. Multiple models were chosen as the 'top models' only if their R^2 values were ≤ 0.1 apart.

Although this is an arbitrary cutoff, this ensures that models explaining similar variation in my data were included as possible explanations.

Simple linear models were also developed to determine the relationship between the flow parameters and species diversity, reproductive-guild diversity, abundances of reproductive guilds and taxonomically-similar subsets. Diversity models were completed using OLS simple linear regression because they met the assumptions. The count data for the reproductive guild and reproductive-taxonomy guild had a negative binomial distribution (data variance > mean; Zuur et al. 2009) and was modeled using a Generalized Linear Model (GLM). There are only two assumptions of GLM, independence and representative of the population. To determine the best models for all fish-assemblage metrics, all models for each metric were ranked based on their R^2 values (pseudo-R^2 for GLMs was calculated as: $\frac{null\ deviance - residual\ deviance}{null\ deviance}$ Zuur et al. 2009). Top models were selected only if their R^2 were ≥ 0.20, deeming them biologically relevant. Multiple top models were selected for each fish-assemblage metric if the R^2 values were ≤ 0.1 apart.

RESULTS

Correlation analyses. Twenty three flow variables were removed though consideration of the species ecology, parameter interpretability, and variable correlations, leaving 10 ecologically meaningful and uncorrelated metrics (Table 2). Because most rivers in the region are groundwater dependent, many did not have zero-flow days and thus, I omitted that parameter from consideration. I retained month flow parameters that would affect the spawning success of the majority of species (period of March – July; Pflieger 1997;

Miller and Robison 2004) and omitted others (August – Feb) to reduce variables included in my models. May and June average flows were correlated (*rho* = 0.80) and May flows were kept to represent this period. High-pulse duration and average March flows were correlated (*rho* = 0.72) but high-pulse duration was kept because I anticipated it would be important for many species that spawn on clean substrate (i.e., lithophils, phytolithophils). Remaining frequency and duration parameters were retained as they were not highly correlated with other parameters. Parameters describing flow magnitude were most often correlated but three metrics were retained. Reversals were correlated with low-pulse frequency (*rho* = 0.70) and reversals were retained because many studies have found this parameter to be ecologically important (Kennen et al. 2008, McManamay et al. 2013), whereas low pulses in groundwater-dependent streams have not been significant (Poff 1996). No parameters describing flow timing or rate of change were highly correlated.

Alteration Indices. Flow alteration indices for the 10 uncorrelated parameters showed both increased and decreased changes from the unaltered to the altered period (Appendix 2). Low-pulse duration was the most altered parameter and showed both increases and decreases from normal (-83% – 362%). For example, the low-flow duration at Lindley Creek increased from an average of 4.3 days to 19.2 days, resulting in an alteration index of 362%. High-pulse duration increased at 12 of 14 sites (-12% – 54%), but two sites showed decreases (Elk and Illinois River). The timing of flow events (minimum and maximum date) were the least altered (-13% – 13%; -29% – 10%, respectively) and were not important flow variables for any of my abiotic or biotic models. All sites, except Spring River, had reductions in rise rate (-66% – 82%), however this was not an

important flow variable for any of my models. Average May flows were both positively and negatively altered (-57% – 88%). Three-day minimum and maximum flows were both positively and negatively altered (-34% – 124%; -49% – 59%) and were the most important flow parameters for 13 of my 24 models. Reductions in high-pulse frequency occurred at all sites, except Baron Fork, (-34% – 3%) and were an important flow parameter for many of my abiotic and biotic models.

Flow-abiotic relationships. Regression models indicated significant relationships between flow alteration indices and a subset of the four abiotic factors (deposited sediment, channel-unit diversity, residual-pool depth, and bankfull width-to-depth ratio; Figure 2). Deposited sediment decreased with increasing three-day minimum flows ($F = 9.313$, $P \leq 0.01$, $R^2 = 0.45$) and high-pulse frequency ($F = 9.674$, $P \leq 0.01$, $R^2 = 0.46$). Channel-unit diversity was positively related to the number of reversals ($F = 7.804$, $P = 0.02$, $R^2 = 0.40$). Residual-pool depth was positively related to high-pulse frequency ($F = 4.408$, $P = 0.06$, $R^2 = 0.25$). No ecologically meaningful models were developed for bankfull width-to-depth ratio.

Flow-biotic relationships. The OLS regression models for diversity metrics showed clear-positive relationships with maximum three-day flow to stream-fish diversity ($F = 14.51$, $P = 0.002$, $R^2 = 0.51$) (Figure 3). Lithophil fishes ($F = 13.45$, $P \leq 0.01$, $R^2 = 0.49$), phytolithophil fishes ($F = 8.77$, $P \leq 0.01$, $R^2 = 0.37$) and speleophil fishes ($F = 8.688$, $P \leq 0.01$, $R^2 = 0.37$) were positively related to maximum three-day flows (Figure 3). Polyphil diversity was not ecologically related to any of the flow metrics.

Several flow-ecology relationships (GLM models) for reproductive guilds were ecologically meaningful and had effect sizes ≥ 0.20 (Figure 4). The relationships of many

of the models were curvelinear, suggesting a possible alteration threshold. Increased duration of both low ($P \leq 0.01$, pseudo-$R^2 = 0.36$) and high flows ($P \leq 0.01$, pseudo-$R^2 = 0.36$) were negatively related to lithophil abundance. Although the diversity of phytolithophils and speleophils increased with maximum three-day flows, their abundance actually decreased with increased maximum three-day flows (phytolithophil: $P \leq 0.01$, pseudo-$R^2 = 0.52$; speleophil: $P \leq 0.01$, pseudo-$R^2 = 0.47$). Polyphil abundances decreased as three-day minimum flows increased ($P \leq 0.01$, pseudo-$R^2 = 0.5$).

Separating the reproductive guilds into smaller taxonomically-based groups provided further insight into how groups of species responded to flow alteration (Figure 5 – 8). The lithophil minnows (14 species, Appendix 3) were the most abundant species within the broad lithophil guild and their abundance had the same negative relationship with low-pulse duration ($P \leq 0.01$, pseudo-$R^2 = 0.46$, Figure 5). However, the lithophilic darter (5 species, Appendix 3) abundance increased as the number of flow reversals increased ($P \leq 0.01$, pseudo-$R^2 = 0.29$, Figure 5) and the lithophilic sucker (4 species, Appendix 3) abundance increased as high-pulse frequencies increased ($P \leq 0.01$, pseudo-$R^2 = 0.38$, Figure 5). The most abundant taxonomic group within the phytolithophil guild were minnows (4 species, Appendix 4) and their abundance was negatively related to maximum three-day flows ($P \leq 0.01$, pseudo-$R^2 = 0.37$, Figure 6). Phytolithophilic darter (2 species, Appendix 4) abundance increased when three-day minimum flow increased ($P \leq 0.01$, pseudo-$R^2 = 0.38$, Figure 6) and when high-pulse frequency increased ($P \leq 0.01$, pseudo-$R^2 = 0.28$, Figure 6, Figure 6). Polyphil sunfish (5 species, Appendix 5) was the most abundant polyphil group and their abundances increased with minimum three-day flows ($P \leq 0.01$, $R^2 = 0.57$, Figure 7). Whereas, the polyphilic bass abundances (3 species,

Appendix 5) increased with three-day maximum flows ($P \leq 0.01$, $R^2 = 0.23$, Figure 7) and average May flows ($P = 0.02$, $R^2 = 0.25$, Figure 7). Catfishes were the only common speleophil taxonomic group across samples (5 species, Appendix 6). Speleophil catfishes had the same relationship to maximum three-day flow ($P \leq 0.01$, $R^2 = 0.42$, Figure 8) as the broader speleophil guild. Catfish abundance was negatively related to maximum three-day flows ($P \leq 0.01$, $R^2 = 0.42$, Figure 8) and average May flows ($P \leq 0.01$, $R^2 = 0.44$, Figure 8).

DISCUSSION

My results showed the majority of flow-ecology models were primarily influenced by magnitude and other dynamic flow conditions. Of the guild relationships tested, I found that three-day maximum and three-day minimum were most often the significant flow metrics (significant in 13 of 24 models). Three-day maximum and minimum represent the seasonal magnitude of rivers at both high and low flows. Similarly, many studies have found magnitude to be an important flow parameter for stream fishes because it increases the quantity and quality of stream habitat (Lytle and Poff 2004; Craven et al. 2010; Poff and Zimmerman 2010). Interestingly, reduced high-pulse frequencies was influential in four models even though it was one of the least altered flow parameters, showing that even low alteration of high-pulse frequency can influence abiotic and biotic stream components. The importance of high-pulse frequencies is probably because it acts as a disturbance event, maintaining dynamic river habitat and communities (Young and Huryn 1996), especially benthic communities (Clausen and Biggs 1997). The annual date of minimum and maximum flows was not an important flow parameter for any of my models, probably because low alteration levels of this parameter do not negatively

influence stream fish assemblages (Yang and Qiang Liu 2012). However, rise rate was reduced at most rivers (13 of 14 sites) but still was not an important variable in any of my models. Although reduced rise rate or 'flashiness' did not influence stream fish assemblages, I anticipate that increased rise rate through hydropower generation would have a greater negative influence on fish assemblages (Kinsolving and Bain 1993; Olivares et al. 2015). Understanding which aspects of the flow regime are most influential on stream fish and habitat is the first step in developing flow-ecology relationships.

Flow magnitude is one of the most altered parameters below reservoirs with alterations to both maximum and minimum flows due to high-flow captures and subsequent releases during low flows (Magilligan and Nislow 2005; Carlisle et al. 2011). Interestingly, both magnitude increases and decreases were found to be important for the natural function of my study sites, similar to a synthesis of almost 100 flow-ecology studies (Poff and Zimmerman 2010). My results showed that both the overall fish diversity and the diversity of certain reproductive guilds (lithophil, phytolithophil, speleophil) were reduced with decreased flow magnitude (three-day maximum flows). My results, along with other studies show that maintaining magnitude below reservoirs is necessary to maintain stream-fish diversity (Carlisle et al. 2010; Kiernan et al. 2012). Although overall fish diversity increased with flow magnitude, phytolithophil and speleophil guild abundances showed the opposite relationship. Increased flow magnitude, including high-pulse events, acts as natural disturbances to stream systems (Lytle and Poff 2004). These natural disturbances increase diversity while preventing single species from becoming overly abundant (i.e., intermediate disturbance hypothesis; Townsend and

Scarsbrook 1997). The inverse relationship of three-day maximum flow on guild diversity and abundance could occur because increased magnitude reduces the abundance of certain species opening niches for other species to persist in those areas. Similarly, other studies have found that increased magnitude negatively influences stream-fish abundances (Freeman et al. 2001; Rolls and Arthington 2014). Results from my research and many other studies have found that increased magnitude is the primary flow component maintaining stream diversity; however other flow regime characteristics are important for maintaining species abundance.

Flow-ecology relationships of the reproductive guild abundances were differentially influenced by various flow metrics. For example, polyphil abundances were related to increases in minimum magnitude flows (i.e., three-day minimum), whereas lithophil abundances increased with reduced duration of high and low flows. These results are consistent with work by Niu et al. (2012), who found that Centrachidae (i.e., polyphil) species were positively related to high-flow magnitudes. Also, species in the family Cyprinidae, comprising many lithophilic species, were related to high and low flow duration (Niu et al. 2012). Red Shiner *Cyprinella lutrensis*, an abundant native phytolithophil species increased in abundance in relation to reduced discharge (Propst and Gido 2004). I also found that phytolithophils increased as maximum flows decreased (i.e., three-day maximum). Although the broad reproductive guilds (lithophil, phytolithophil, polyphil, speleophil) were significantly related to aspects of the flow regime, many taxonomically different species occur in each reproductive guild. As expected, guild abundances often comprised a few abundant species and several less abundant species. McManamay and Frimpong (2015) indicated that broad fish guilds

could be too coarse to detect certain flow-ecology relationships that could potentially be detected with finer guilds. Ecologically similar species may also respond differently to flow regime (Freeman et al. 2001; Wenger et al. 2008), suggesting coarser reproductive guilds may not always be representative for inclusive species. A promising approach to examining species responses to flow alteration is to group fishes with similar traits (e.g., morphological and reproductive).

To my knowledge, I am the first to determine the relationship between both coarse-reproductive guilds and a more fine-scale subset of species and flow alteration. Flow alteration does not influence riverine fishes uniformly and certain species and guilds are adapted to different aspects of the flow regime (Krabbenhoft et al. 2014). The lithophil minnows, for example, responded to decreases in high and low-pulse duration as the broader guild. However, lithophil darters were positively related to reversals, whereas lithophil suckers were positively related to high-pulse frequency. Previous studies have found that species in the Catostomidae (i.e., suckers) and Percidae (i.e., darters) families were more influenced by high discharge events, whereas Cyprinidae (i.e., minnows) were more related to positive and negative duration changes of high and low flows (Niu et al. 2012). Sucker species, like all lithophils, require clean substrate for spawning, but they may be better able to thrive in habitats with high pulses because they are morphologically adapted to handle high discharge. For example, the wide pectoral fins (Lundberg and Marsh 1976), and sucker mouth shape allows suckers to have superior swimming abilities in high-velocity habitats (Ward et al. 2003). One reason darters may be related to dynamic high-flows events could be because they rely on multiple habitat components (i.e., riffle and pools) to complete their life cycle, whereas many minnows do not (Kanno

and Vokoun 2010). The phytolithophil minnows increased with decreases in three-day maximum flows; however, darter abundance increased with higher minimum flows (i.e., three-day minimum) and high-pulse frequency. Reduced flow magnitude often allows active swimmers, such as minnows, to replace benthic fishes (i.e., darters) (Carslisle et al. 2010). The taxonomic-reproductive guilds not only provide information on the flow-ecology differences between fine-scale guilds, they are still broad enough to apply across broad scales and also reflect important habitat differences within the broader defined guild.

Interestingly, many of the relationships between taxonomic-guild subsets and flow mirrored those with the abiotic measurements. For example, lithophilic suckers and deposited sediment were both related to high-pulse frequency. Lithophils require clean substrates for successful spawning (Balone 1975; Berkman and Rabeni 1987; Poff et al. 1997) so it is not surprising that flow metrics reducing fine sediment would also benefit this guild. However, suckers in particular appeared to be more influenced by deposited sediment than the other taxonomic groups within the lithophil guild. Freeman et al. (2001) found that redhorse *Moxostoma spp* abundances decreased below regulated rivers and postulated this was due to reduced suitable habitat. Similarly, phytolithophilic darters were sensitive to increases in deposited sediment, which fills the interstial spaces of substrate (Berkman and Rabeni 1987) and reduces aquatic vegetation (Gleason et al. 2003). Darter morphology is adapted to occupy fast-flowing riffle habitat, allowing them to benefit from improved habitat due to high flows (Matthews 1985). I also found that lithophilic darters had the same relationship to flow reversals as channel-unit diversity. Similarly, Meador and Carlisle (2012) found that riffle-dwelling species (i.e., darters)

were more susceptible to reductions in natural flow variability (i.e., reversals). These findings support the importance of the abiotic metrics that were chosen and suggest they could be useful to measure across Arbuckle Mountain and Ozark Highland streams as predictive measures of fish-assemblage alterations.

The relationships between deposited sediment, channel-unit diversity and residual-pool depth with various flow metrics suggests these are useful abiotic indicators for predicting future flow-management problems. Channel-unit diversity, for instance, has been shown to be positively related to Smallmouth Bass abundance (Sowa and Rabeni 1993; Brewer 2013), which I found to be negatively related to flow stability. The diversity of channel units is maintained by high-flow events (Gordon, 2004) and supports prey abundance for many stream fishes (e.g., crayfish, Brewer et al. 2009). When flows cease during summer, Smallmouth Bass abundance decline presumably due to lack of food (Hafs et al. 2010). Residual-pool depth has been shown to be a significant descriptor of pool quality (Ralph et al. 1994; Bauer and Ralph 2001) and related to the abundance of several native fish species (Peterson and Rabeni 2001). I found reductions in the frequency of high-pulse flows related to higher amounts of instream deposited sediment. Several studies have also shown that high-pulse frequency relates to decreases in deposited sediment (Xu et al. 2005; Kennen et al. 2008). Others have found sediment increases when the opposite metric (low-flow duration) increases (Dewson et al. 2007; Martinez-Capel et al. 2013). These abiotic flow-ecology relationships can provide important indicators of stream-ecological conditions.

The relationships between the flow regime and habitat allows for measurements of stream habitat to be used as an index of flow alteration and its effects on stream biota

(Cavendish and Duncan 1986; Jowett 1990; Beecher et al. 1993). Agencies often do not have the resources (i.e., money, time, labor) to sample fishes in every river annually (Barbour et al. 1999). It is much more efficient to quickly measure stream habitat to determine how flow regimes are likely affecting habitat and subsequently future fish assemblages. For example, increased flow stability has been shown to be associated with reductions in microhabitat diversity (Martinez-Capel et al. 2013) and especially riffle habitat (Hakala and Hartman 2004). Also, monitoring fine sediment has important ecological justification because increasing sediment relates to declines in spawning habitat (McDonald et al. 2010), invertebrates (Kennen et al. 2008), and benthic fishes (see Kemp et al. 2011 for a review). I recognize that other factors also affect the physical habitat in streams (e.g., urban land use, cattle grazing) so familiarity with catchment activities is necessary to help tease apart these human alterations (Rolls and Arthington 2014). Further, it is interesting that my findings did not relate flow changes to width-to-depth ratio because this habitat characteristic has been suggested to be indicative of land-use changes (Brewer 2013). These results suggest the abiotic metrics here may be a useful starting point in distinguishing land-use and flow alterations. Further, streams could be targeted for habitat sampling based on flow-alteration levels by using readily-available gage data.

Although the flow regime is unique to each river system, developing flow-ecology relationships and flow standards for groups of similar rivers is more practical for managers (Arthington et al. 2006; Poff et al. 2010). In order to minimize the ongoing declines to native aquatic biota, it is necessary to develop coarse-scale flow standards for groups of similarly functioning rivers. Flow-ecology relationships and flow standards that

are developed with a subset of rivers in a region, allows for extrapolation to ungaged rivers in that same region (Arthington et al. 2006). This is important because most rivers in the U.S. do not have historic USGS gage flow data, which makes it difficult to determine the flow regime of each river (Kennen et al. 2008). However, many tools are becoming available in an attempt to predict flow on ungaged streams (e.g., USGS Streamstats 2012). Grouping similar rivers based on hydrology will not, however, correct for inefficient sampling. Sampling efficiency of gears will differ across abiotic gradients within streams and will influence fish-assemblage results (Peterson and Paukert 2009). Care should be used in developing monitoring plans to reduce variation in sampling efforts (e.g., sample under similar discharge conditions at the same time of year, use of multiple gears to minimize bias) or by calibration of gears based on known efficiencies (Peterson and Paukert 2009). Species detection probability varies based on abiotic stream characteristics and more research is necessary to prevent sampling biases from influencing flow-ecology relationships, leading to inappropriate inferences (Beesley et al 2014, Gwinn et al. 2015).

Despite several limitations, implementing flow standards is an important first step to preventing loss of aquatic species diversity and abundance. More research is needed to determine the transferability of flow-ecology relationships and environmental-flow standards across streams with similar hydrologic classifications (Gillespie et al. 2015), especially at ungaged sites. For example, abrupt changes in channel morphology (caused by urbanization or other factors; Deng et al. 2015) might change the flow-ecology relationships. Another limitation of most flow-ecology studies is that data are often based on single sampling events because temporal replication and historic fish assemblage data

at sites across various flow regimes is rare (Kiernan et al. 2012). Finally, although my research determined flow-ecology relationships for three abiotic characteristics, there are many other aspects of stream habitat that are altered due to flow regulation, such as temperature (King et al. 2015). Despite these knowledge gaps, the importance of developing flow standards should not be understated. Such standards would aid in preserving the natural structure and function of lotic systems, consequently, preventing the continued decline of native biota. These relationships serve as starting points to begin the process of flow management within an adaptive-management framework.

Table 1. Mean (standard deviation) habitat characteristics (Bankfull width-to-depth ratio, residual-pool depth, and deposited sediment) from 14 rivers in the Arbuckle Mountain and Ozark Highland ecoregions. Channel-unit diversity was calculated using Shannon-Weiner diversity index: $H = -\Sigma PlnP$ (P = species proportion; Begon et al. 2006).

River	Channel Unit Diversity	Bankfull Width-Depth Ratio	Residual Pool Depth (m)	Deposited Sediment (%)
Spavinaw Creek	2.50	39 (12)	1.11 (0.87)	31 (0.04)
Illinois River	2.44	35 (8)	1.33 (0.2)	10 (4.3)
Baron Fork	3.75	66 (20)	2.25 (0.5)	17 (0.05)
Turnback Creek	3.01	29 (8)	00.9 (0.3)	20 (0.01)
Little Sac River	3.19	36 (2)	0.75 (0.13)	11 (0.06)
Lindley Creek	2.68	34 (7)	0.83 (0.2)	9 (0.07)
Little Piney River	3.10	32 (2)	0.87 (0.06)	30 (0.03)
Spring River	1.19	81 (21)	1.27 (0.3)	5 (0.24)
Elk River	1.43	97 (55)	1.08 (0.2)	15 (6.5)
Washita River downstream	2.13	70 (10)	1.09 (0.57)	49 (10.4)
Washita River upstream	1.89	43 (12)	1.41 (0.48)	27 (11.3)

Table 2. Uncorrelated Indicators of Hydrologic Alteration (IHA) flow parameters used to develop flow-ecology relationships for habitat and reproductive guilds of fishes.

IHA Flow Parameter	Flow Regime Component	Description of Parameter
May	Magnitude	Mean monthly flows in May
Three-Day Max	Magnitude	Mean of annual three day maximum flows
Three-Day Min	Magnitude	Mean of annual three day minimum flows
High-Pulse Frequency	Frequency	Number of high pulses within a year
High-Pulse Duration	Duration	Mean duration of high pulse flows
Low-Pulse Duration	Duration	Mean duration of low pulse flows
Date Max	Timing	Julian date of one day maximum flow
Date Min	Timing	Julian date of one day minimum flow
Rise Rate	Rate of Change	Mean difference between all consecutively increasing flows
Reversals	Rate of Change	Number of hydrologic reversals

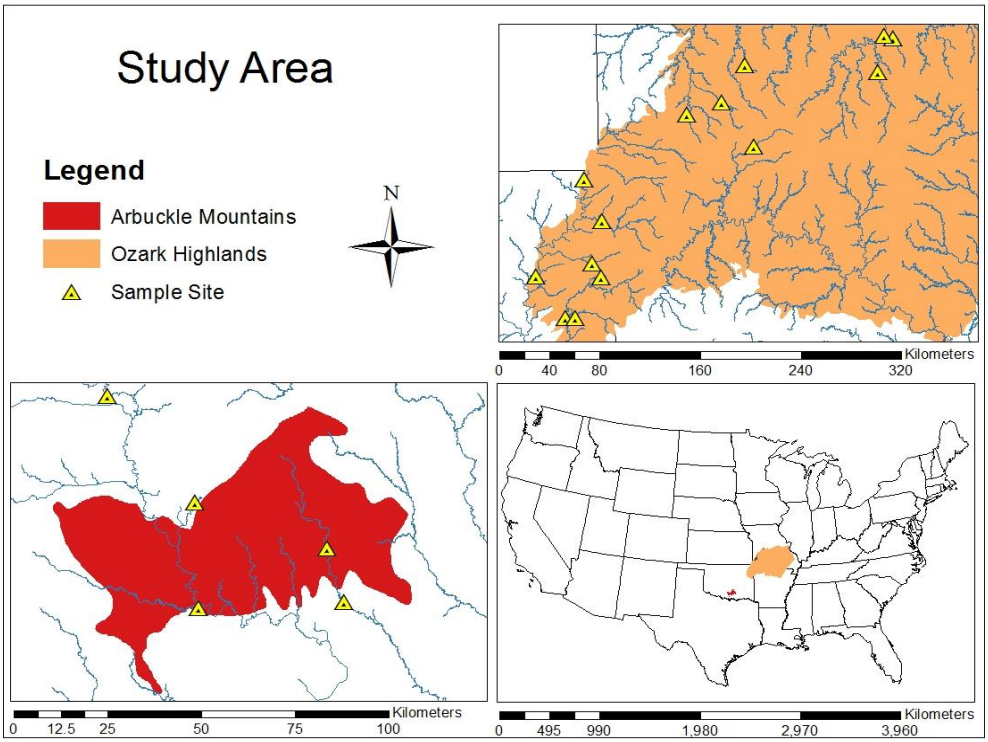

Figure 1. Sample sites, located in the Arbuckle Mountain (red) and Ozark Highland (orange) ecoregions, USA, where fish and habitat measurements were taken to develop flow-ecology relationships.

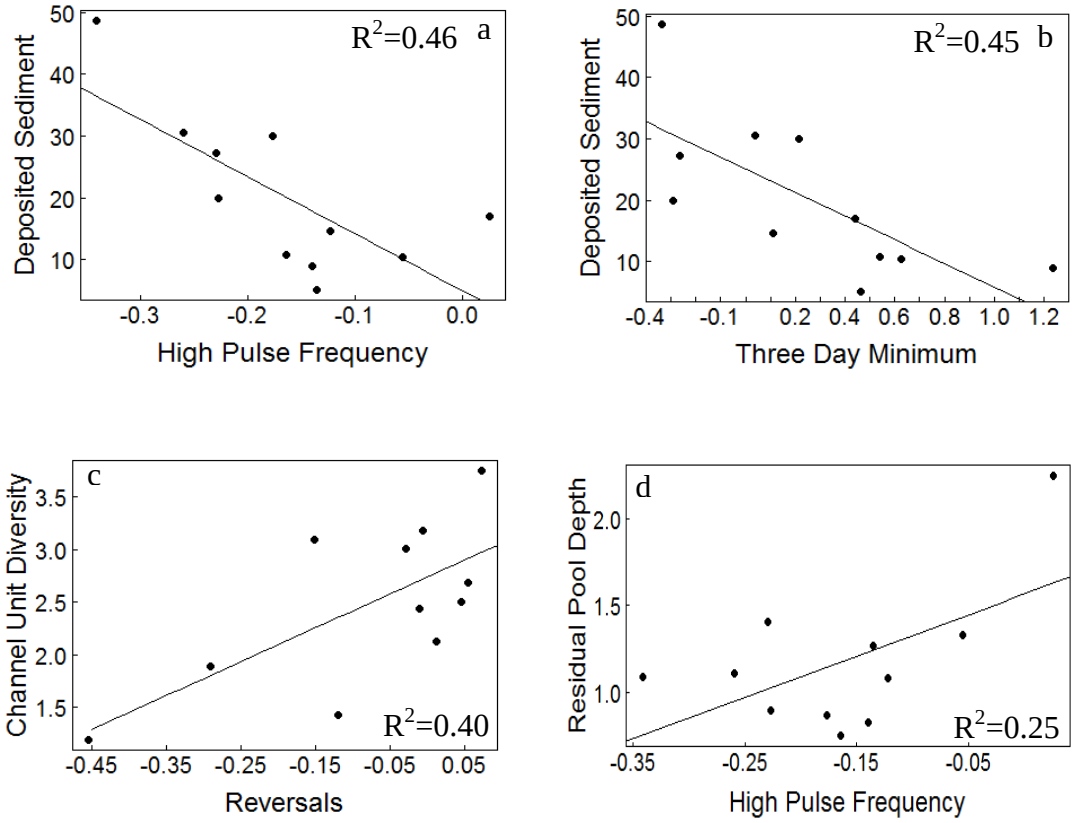

Figure 2. A flow-alteration index was used in place of all flow parameters and was calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the linear relationship between deposited sediment and a) high-pulse frequency (the number of high flow events annually) and b) three-day minimum (average minimum flows over three days). Panel c shows the relationship between channel-unit diversity and reversals (number of high and low flow events annually). Panel d shows the relationship between residual-pool depth and high-pulse frequency (number of annual high flow events).

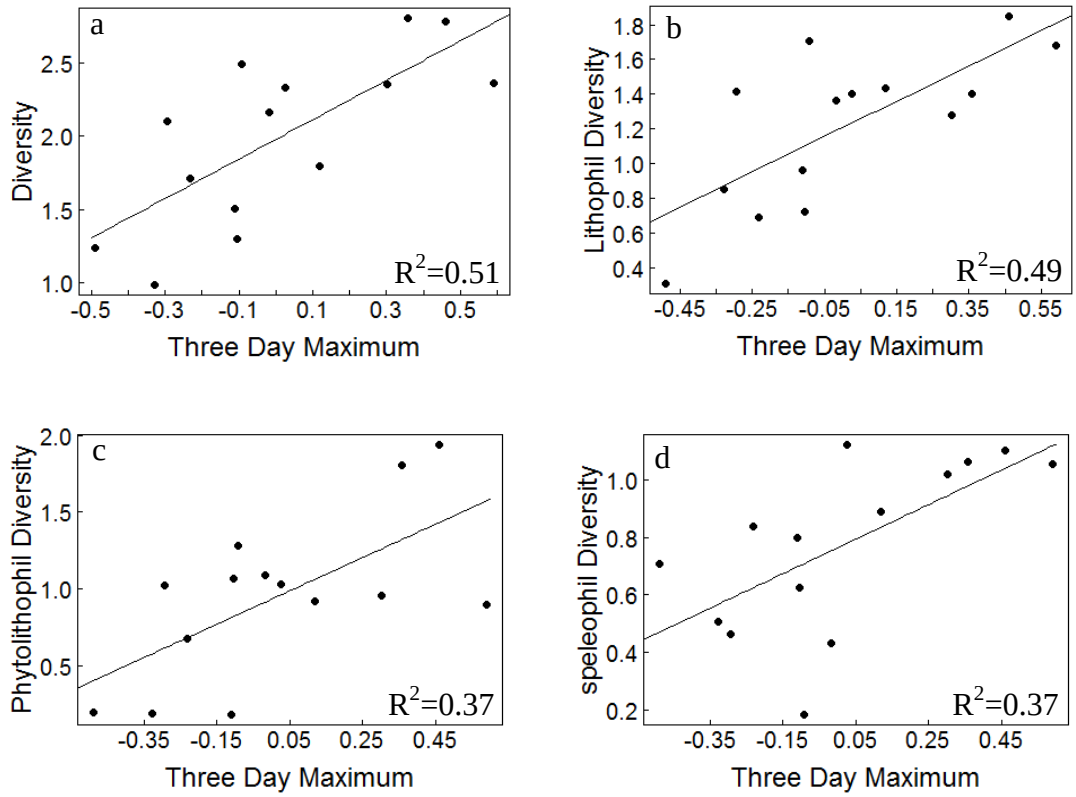

Figure 3. A flow-alteration index was used in place of all flow parameters and was calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the linear relationship between three-day maximum (average maximum flow over three days) and a) stream fish diversity, b) lithophil reproductive guild (fishes that spawn on clean gravel-cobble substrate) diversity, c) phytolithophil reproductive guild (fishes that spawn on gravel-cobble substrate and aquatic vegetation) diversity, and d) speleophil reproductive guild (fishes that spawn in crevices and pores of stream channel) diversity.

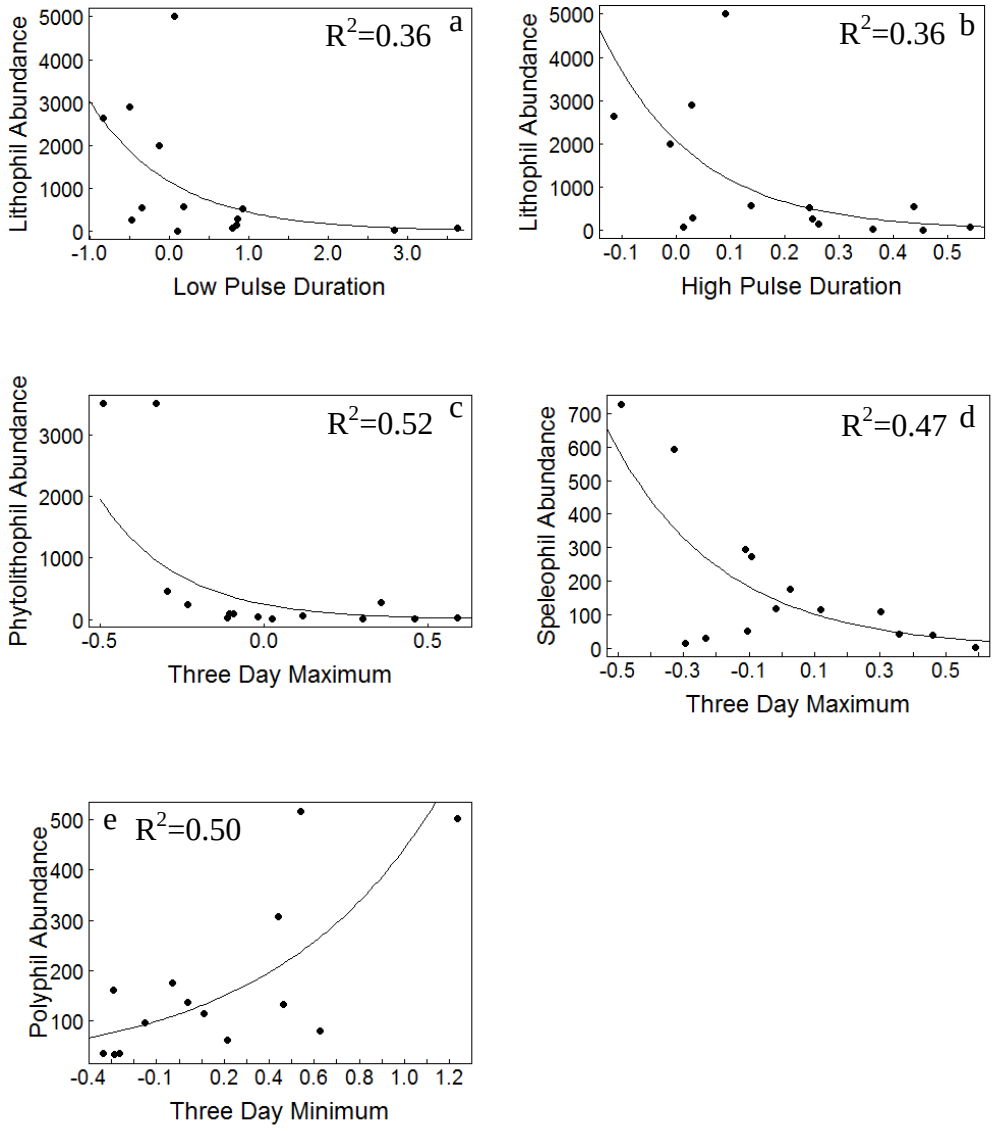

Figure 4. A flow-alteration index was used in place of all flow parameters and calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the relationship between lithophil (spawn on clean gravel-cobble substrate) abundance and a) high-pulse duration and b) low-pulse duration. Panels show the relationship between c) phytolithophil (spawn on aquatic vegetation and gravel-cobble substrate) and d) speleophil (spawn on crevices in river) with three-day maximum. Panel e shows the relationship between polyphil (build and spawn on substrate nests) abundance and three-day minimum.

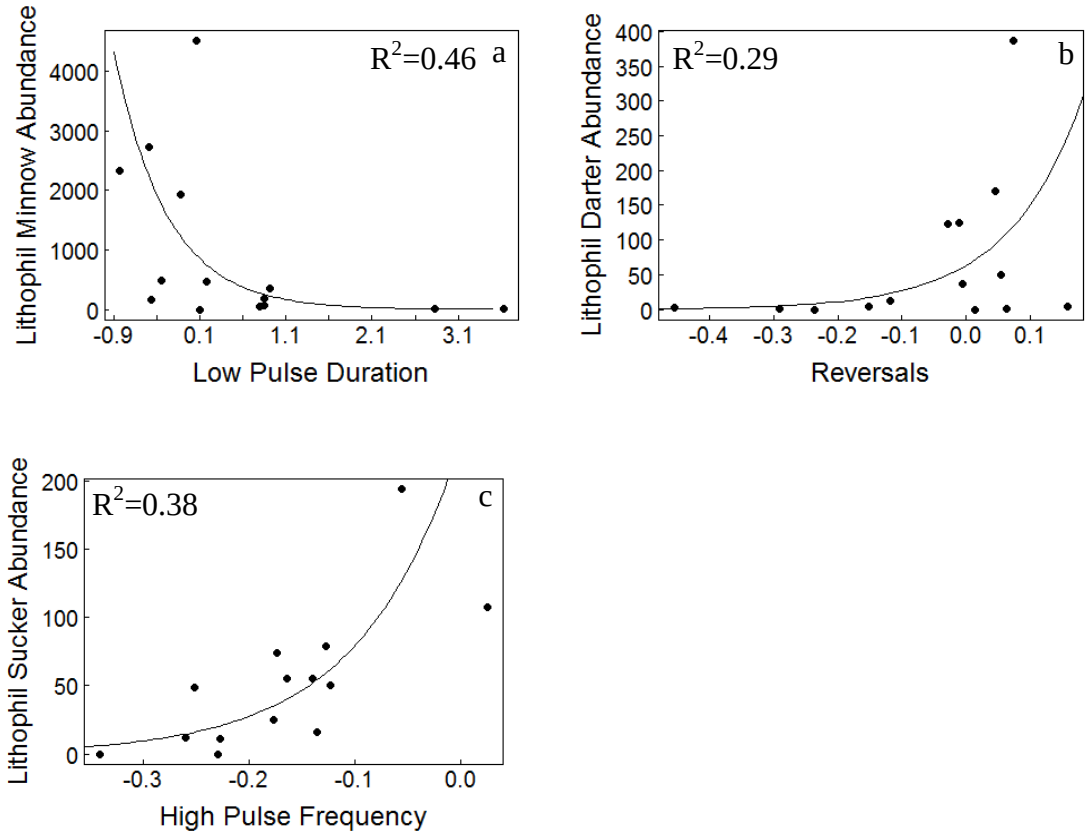

Figure 5. A flow-alteration index was used in place of all flow parameters and calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the curvilinear relationship between lithophil minnows and a) low pulse duration, lithophil darters and b) reversals (number of high and low flow events annually), and litophil suckers and c) high pulse frequency (the number of high pulse events annually).

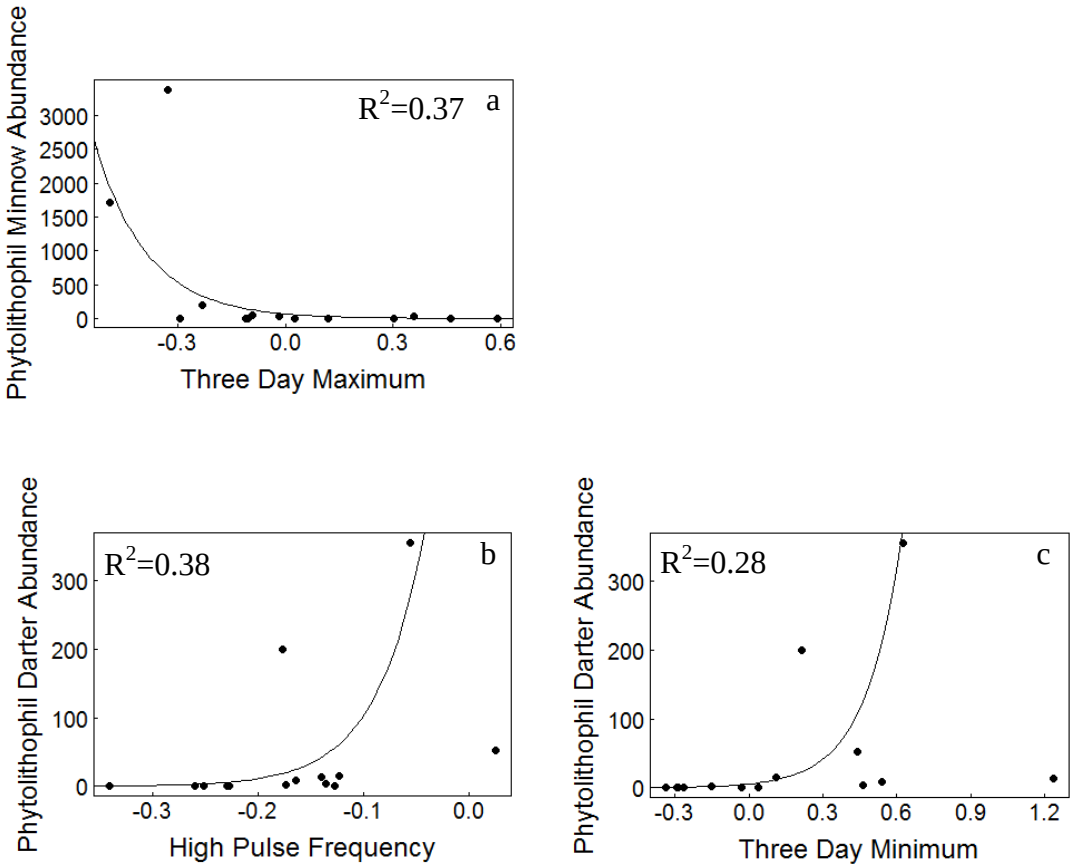

Figure 6. A flow-alteration index was used in place of all flow parameters and calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the curvilinear relationship between phytolithophil minnows and a) three day maximum flow, phytolithophil darters and b) three day minimum (average minimum flow over three days), and c) high pulse frequency (number of high pulse events annually).

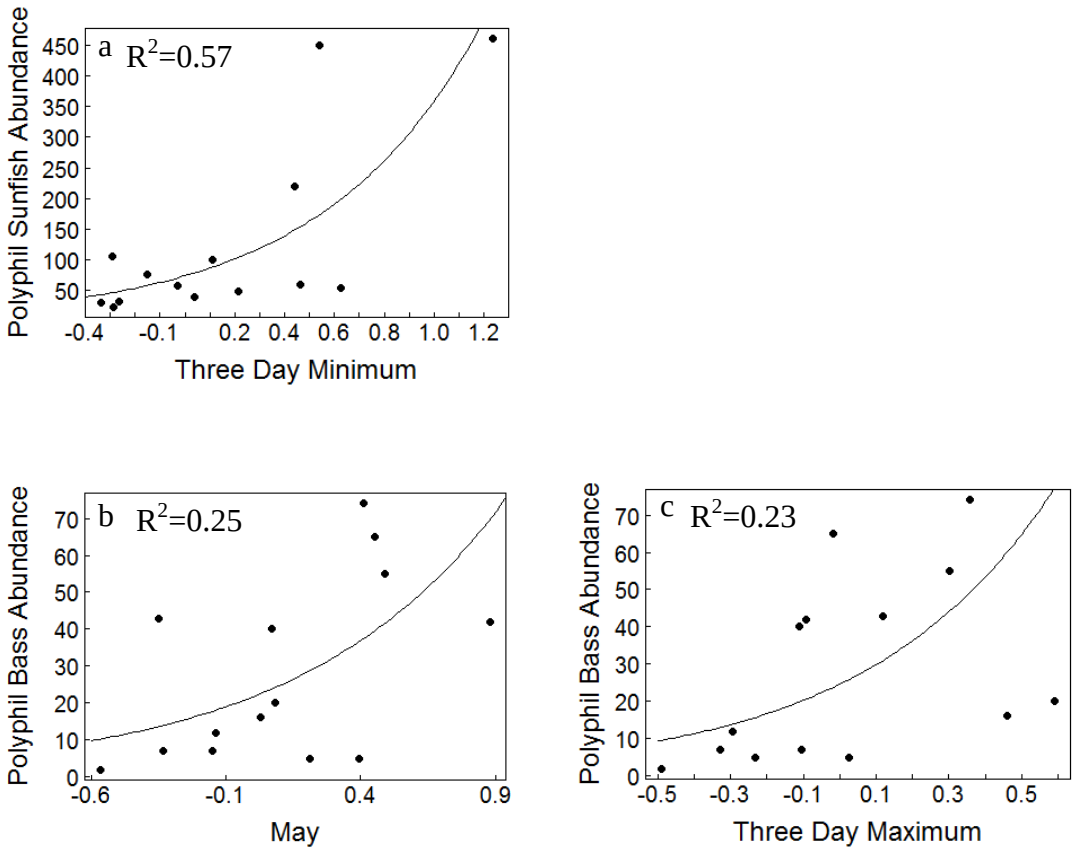

Figure 7. A flow-alteration index was used in place of all flow parameters and calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the curvilinear relationship of polyphil sunfishes and a) three day minimum flow and between polyphil basses and b) average May flows and c) three day maximum flow (average maximum flows over three days).

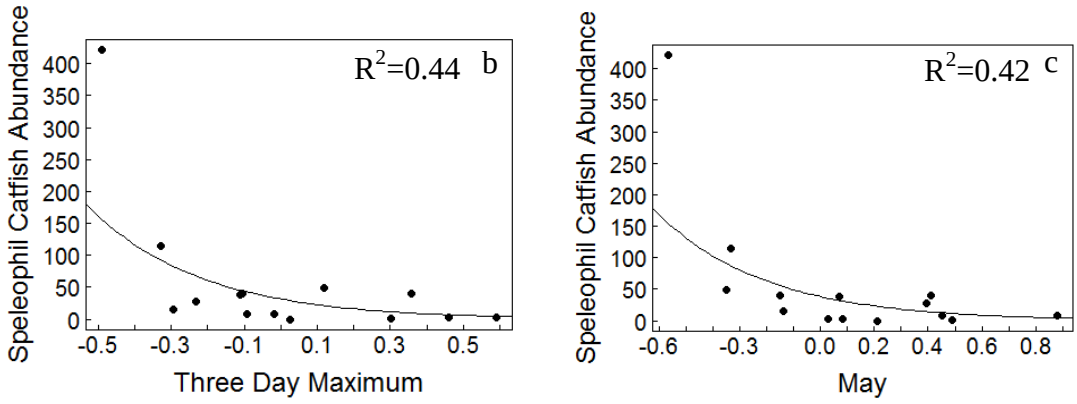

Figure 8. A flow-alteration index was used in place of all flow parameters and calculated as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013). Panels show the curvilinear relationship between speleophil catfish and a) three day maximum flow and b) average May flow.

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APPENDICES

Appendix 1. Average flows of the 10 uncorrelated parameters from Indicators of Hydrologic Alteration (IHA) for unaltered and altered time periods of 14 rivers in the Arbuckle Mountain and Ozark Highland ecoregions.

River	May	3 Day Min	3 Day Max	Date Min	Date Max	HPF	LPD	HPD	Rise Rate	Reversals
Baron Fork (1949-1963)	434	20	5017	269	138	7.9	14.9	7.8	26	61
Baron Fork (2001-2015)	283	28	5620	253	144	8.1	15.8	8.5	17	65
Illinois River (1936-1950)	1226	96	19628	280	153	8.4	30.4	7.5	73	75
Illinois River (2001-2015)	1059	156	13834	257	143	7.9	5.0	6.7	60	74
Spavinaw Creek (1962-1976)	105	14	1739	247	155	6.9	42.3	8.4	8	44
Spavinaw Creek (2001-2015)	112	14	1545	242	122	5.1	21.4	8.7	5	46
Spring River (1956-1976)	1957	131	23323	274	151	10.3	3.6	4.2	98	152
Spring River (2001-2015)	2769	192	31685	264	142	8.9	13.9	5.8	179	83
Elk River (1940-1954)	1115	77	13681	253	123	7.1	19.9	8.6	69	70
Elk River (2001-2015)	950	86	12252	260	135	6.2	17.3	8.5	46	62
Turnback Creek (1965-1979)	213	28	2148	262	162	7.9	13.8	6.1	28	69
Turnback Creek (2001-2015)	316	20	2799	269	138	6.1	26.5	7.6	17	67
Little Sac River (1969-1983)	151	6	3010	245	149	9.7	12.2	4.4	23	82
Little Sac	218	10	2959	247	151	8.1	14.4	5.0	15	81

River (2001-2015)										
Little Piney Creek (1929-1943)	176	40	2335	252	182	11.3	7.4	3.2	11	107
Little Piney Creek (2001-2015)	213	48	2393	238	139	9.3	4.8	4.6	10	90
Big Piney Creek (1922-1936)	517	115	5456	258	175	10.5	6.3	5.4	56	104
Big Piney Creek (2001-2015)	560	112	8682	228	161	9.1	11.6	5.6	19	79
Lindley Creek (1958-1972)	41	0.28	2022	242	186	14.3	20.6	2.9	10	84
Lindley Creek (2001-2015)	78	0.63	1832	255	132	12.3	10.9	3.7	7	89
Gasconade River (1918-1933)	3063	545	25399	252	144	9.2	7.1	6.6	375	72
Gasconade River (2001-2015)	3150	463	37103	270	140	7.6	13.1	8.4	135	84
Neosho River (1940-1954)	3873	99	51619	245	155	12.7	9.9	3.7	488	90
Neosho River (2001-2015)	5407	70	39606	278	144	9.5	10.9	5.3	326	96
Washita Upstream (1938-1952)	1858	102	11285	275	180	9.6	4.2	5.2	54	128
Washita Upstream (2001-2015)	807	75	5751	240	194	7.4	19.3	5.2	36	90
Washita Downstream (1929-1943)	2857	143	20420	254	154	11.3	6.1	5.7	171	90
Washita Downstream (2001-2015)	1908	95	13688	248	145	7.5	11.0	8.7	93	91

Appendix 2. Alteration index of 10 uncorrelated flow parameters from Indicators of Hydrologic for 14 rivers in the Arbuckle Mountain and Ozark Highland ecoregions. Alteration index for each flow parameter as: $\frac{altered\ flows - unaltered\ flows}{unaltered\ flows}$ (Belmar et al. 2013).

River	May	3 Day Min	3 Day Max	Date Min	Date Max	HPF	LPD	HPD	Rise Rate	Reversals
Baron Fork	-0.35	0.44	0.12	-0.06	0.05	0.03	0.06	0.09	-0.36	0.07
Illinois River	-0.14	0.62	-0.30	-0.08	-0.07	-0.06	-0.83	-0.12	-0.17	-0.01
Spavinaw Creek	0.07	0.04	-0.11	-0.02	-0.21	-0.26	-0.49	0.03	-0.34	0.05
Spring River	0.41	0.46	0.35	-0.04	-0.06	-0.14	2.83	0.36	0.82	-0.45
Elk River	-0.15	0.11	-0.10	0.03	0.10	-0.12	-0.13	-0.01	-0.34	-0.12
Turnback Creek	0.48	-0.29	0.30	0.03	-0.15	-0.23	0.92	0.25	-0.40	-0.03
Little Sac River	0.45	0.54	-0.02	0.01	0.01	-0.16	0.18	0.14	-0.34	-0.01
Little Piney Creek	0.21	0.22	0.03	-0.06	-0.23	-0.18	-0.34	0.44	-0.10	-0.15
Big Piney Creek	0.08	-0.03	0.59	-0.12	-0.08	-0.13	0.85	0.03	-0.66	-0.24
Lindley Creek	0.88	1.24	-0.09	0.06	-0.29	-0.14	-0.47	0.25	-0.29	-0.08
Gasconade River	0.03	-0.15	0.46	0.07	-0.03	-0.17	0.85	0.26	-0.64	0.16
Neosho River	0.40	-0.29	-0.23	0.13	-0.07	-0.25	0.10	0.45	-0.33	0.06
Washita Up stream	-0.57	-0.26	-0.49	-0.13	0.08	-0.23	3.62	0.01	-0.34	-0.29
Washita Down stream	-0.33	-0.34	-0.33	-0.02	-0.06	-0.34	0.79	0.54	-0.45	0.01

Appendix 3. Common name, scientific name, taxonomy group and total count from 14 rivers in the Arbuckle Mountain and the Ozark Highland ecoregions for the lithophil reproductive group (fishes that spawn on clean gravel-cobble substrate).

Common Name	Scientific Name	Taxonomy	Total Count
Common Logperch	*Percina caprodes*	Darter	162
Dusky Darter	*Percina sciera*	Darter	1
Orangethroat Darter	*Etheostoma spectabile*	Darter	689
Slenderhead Darter	*Slenderhead Darter*	Darter	5
Stippled Darter	*Etheostoma punctulatum*	Darter	57
Bigeye Chub	*Hybopsis amblops*	Minnow	51
Bigeye Shiner	*Notropis boops*	Minnow	24
Bleeding Shiner	*Luxilus zonatus*	Minnow	609
Cardinal Shiner	*Luxilus cardinalis*	Minnow	6108
Central Stoneroller	*Campostoma anomalum*	Minnow	4049
Creek Chub	*Semotilus atromaculatus*	Minnow	45
Ghost Shiner	*Notropis buchanani*	Minnow	1
Gravel Chub	*Erimystax x-punctatus*	Minnow	12
Ozark Minnow	*Notropis nubilus*	Minnow	2097
Redspot Chub	*Nocomis asper*	Minnow	61
Rosyface Shiner	*Notropis rubellus*	Minnow	12
Striped Shiner	*Luxilus chrysocephalus*	Minnow	94
Suckermouth Minnow	*Phenacobius mirabilis*	Minnow	43
Wedgespot Shiner	*Notropis greenei*	Minnow	61
Northern Hogsucker	*Hypentelium nigricans*	Sucker	200
Redhorse	*Moxostoma spp.*	Sucker	463
Spotted Sucker	*Minytrema melanops*	Sucker	3
White Sucker	*Catostomus commersonii*	Sucker	13
Chestnut Lamprey	*Ichthyomyzon castaneus*	Lamprey	2
Lamprey Larvae	*Ichthyomyzon sp.*	Lamprey	14
Orangespotted Sunfish	*Lepomis humilis*	Sunfish	85
Blackspotted Topminnow	*Fundulus olivaceus*	Topminnow	58
Black Bullhead	*Ameiurus melas*	Catfish	3

Appendix 4. Common name, scientific name, taxonomy group and total count from 14 rivers in the Arbuckle Mountain and Ozark Highland ecoregions for the phytolithophil reproductive group (fishes that spawn on gravel-cobble substrate and aquatic vegetation).

Common Name	Scientific Name	Taxonomy	Total Count
Banded Darter	*Etheostoma caeruleum*	Darter	362
Greenside Darter	*Etheostoma blennioides*	Darter	102
Mimic Shiner	*Notropis volucellus*	Minnow	2
Red Shiner	*Cyprinella lutrensis*	Minnow	5391
Silver Chub	*Macrhybopsis storeriana*	Minnow	3
Bigmouth Buffalo	*Ictiobus cyprinellus*	Sucker	3
River Carpsucker	*Carpiodes carpio*	Sucker	89
Smallmouth Buffalo	*Ictiobus bubalus*	Sucker	150
Longnose Gar	*Lepisosteus osseus*	Gar	55
Shortnose Gar	*Lepisosteus platostomus*	Gar	16
Gizzard Shad	*Dorosoma cepedianum*	Shad	273
Brook Silverside	*Labidesthes sicculus*	Silverside	63
White Bass	*Morone chrysops*	Bass	10
Northern Studfish	*Fundulus catenatus*	Topminnow	21

Appendix 5. Common name, scientific name, taxonomy group and total count from 14 rivers from the Arbuckle Mountain and Ozark Highlands ecoregions for the polyphil reproductive group (fishes that build and spawn on substrate nests).

Common Name	Scientific Name	Taxonomy	Total Count
Largemouth Bass	*Micropterus salmoides*	Bass	44
Smallmouth Bass	*Micropterus dolomieu*	Bass	129
Spotted Bass	*Micropterus punctulatus*	Bass	220
Bluegill	*Lepomis macrochirus*	Sunfish	343
Green Sunfish	*Lepomis cyanellus*	Sunfish	208
Longear Sunfish	*Lepomis megalotis*	Sunfish	1178
Redear Sunfish	*Lepomis microlophus*	Sunfish	33
Warmouth	*Lepomis gulosus*	Sunfish	1
Ozark Bass	*Ambloplites constellatus*	Ambloplites	1
Rock Bass	*Ambloplites rupestris*	Ambloplites	227
Black Crappie	*Pomoxis nigromaculatus*	Crappie	7
White Crappie	*Pomoxis annularis*	Crappie	5

Appendix 6. Common name, scientific name, taxonomy group and total count from 14 rivers from the Arbuckle Mountain and Ozark Highland ecoregions for the speleophil reproductive group (fishes that in crevices and pores of stream channel).

Common Name	Scientific Name	Taxonomy	Total Count
Channel Catfish	*Ictalurus punctatus*	Catfish	641
Flathead Catfish	*Pylodictis olivaris*	Catfish	19
Yellow Bullhead	*Ameiurus natalis*	Catfish	11
Slender Madtom	*Noturus exilis*	Catfish	93
Stonecat	*Noturus flavus*	Catfish	2
Blacktail Shiner	*Cyprinella venusta*	Minnow	15
Bluntnose Minnow	*Pimephales notatus*	Minnow	463
Bullhead Minnow	*Pimephales vigilax*	Minnow	794
Fathead Minnow	*Pimephales promelas*	Minnow	1
Spotfin Shiner	*Cyprinella spiloptera*	Minnow	17
Whitetail Shiner	*Cyprinella galactura*	Minnow	12
Banded Sculpin	*Cottus carolinae*	Sculpin	409
Mottled Sculpin	*Cottus bairdii*	Sculpin	21
Ozark Sculpin	*Cottus hypselurus*	Sculpin	36
Fantail Darter	*Etheostoma flabellare*	Darter	66

CHAPTER III

THERMAL TOLERANCE OF STREAM FISHES EXPOSED TO VARYING THERMAL REGIMES

ABSTRACT

Climate change, landscape alteration, and flow regulation alter the natural thermal regime of rivers. Water temperature influences life history of most fishes, including spawning time, metabolism rate, disease and predation susceptibility, and survival. Water temperature has the potential to increase beyond the thermal tolerance of many species, which would result in species dispersal, acclimation, or extirpation. Traditional methods for determining ectothermic temperature tolerance are focused on immediate biological responses without acclimation and thus are not very ecologically meaningful. I determined the critical thermal maxima (CTM) of 15 species and the longer-term temperature tolerance of 10 species of fishes that occupy spring-fed streams of the Arbuckle Mountain ecoregion. During the CTM trials, water temperature was increased 2°C per h until the fish experienced loss of equilibrium and death as the endpoint. CTM ranged 34 – 36°C and species with the highest CTM were mid-channel minnows and sunfish, whereas species with the lowest CTM were spring-fed obligates, Oklahoma species of greatest concern and benthic darters and minnows. Longer-term trials had both

a spring-fed (SF) and a non spring-fed (NSF) treatment and mimicked the average summer diel changes observed in these streams (4°C and 8°C, respectively). Results from the GLM indicated the species by acclimation period interaction was significant meaning species' thermal tolerances differed depending on the length of the acclimation period (CTM D, SF or NSF). Juvenile Bluegill had the highest temperature tolerance for both SF and NSF trials, compared to spring-fed obligates and benthic darters with the lowest temperature tolerance. Seventy percent (7 of 10) of the species had a thermal tolerance approximately 2°C higher in the SF compared to the CTM. Information on the acclimation ability of fishes to increased temperature is important for predicting the sensitivity of long-term temperature changes and forecasting species of conservation concern.

INTRODUCTION

Stream temperatures vary laterally, longitudinally, and vertically and the observed thermal patterns are influenced by the physicochemical character of the associated system. Upstream reaches maintain a cooler temperature than downstream reaches because they are typically shaded by riparian vegetation (Johnson 2004) and are often influenced more by groundwater contributions (Brown et al. 2005). The benthos of streams has a smaller temperature fluctuation when compared to surface water due to interactions with the hyporheic zone (Brown et al. 2005; Schmidt et al. 2006). Diel temperature fluctuations increase in bedrock reaches of streams compared to cobble-gravel substrate (Johnson 2004). Bed substrate type can also influence stream temperature due to its interaction with the hyporheic zone (i.e., coarser substrate has greater pores, increasing groundwater inputs; Brown et al. 2005). Beyond the stream

channel itself, landscape alterations and climate change have the potential to influence the thermal regime of streams in a variety of ways depending on the structure of the lotic system (Poole and Berman 2001).

Stream temperatures have indirect and direct consequences on stream biota. A disturbed thermal regime is anticipated to alter the abundance and diversity of stream fishes (Lyons et al. 2010; Ostrand and Wilde 2001). However, some species may persist in streams with altered thermal regimes but exhibit reduced survival (Ficke et al. 2007) or reproductive output (Webb et al. 2001). In extreme cases, some fishes may become extirpated due to altered thermal conditions (e.g., species living at the edge of the range, Ficke et al. 2007). Indirectly, increased stream temperatures cause fishes to become more susceptible to diseases (Morvan et al. 1998) and predation (Coutant 1976). The toxicity of pollutants to fishes also increases as stream temperatures become warmer (Langford 1990; Caissie 2006). Increased temperature can influence the reproductive timing of freshwater fishes, thereby affecting spawning success, growth and recruitment (Sundararaj and Vasal 1976; Rolls et al. 2013). Temperature also directly affects fish survival by influencing abiotic stream processes. Dissolved oxygen saturation levels are dependent on water temperature and increased temperature could reduce dissolved oxygen below necessary levels for stream fishes to survive (Morrill et al. 2005; Caissie 2006). Increased stream temperatures cause the oxygen demand of fish mitochondria to exceed oxygen availability; thus, their heart cannot circulate enough oxygenated blood for them to survive (Portner 2002). Despite the important role that temperature plays in the lives of fishes, very little is known about the maximum temperature tolerance of most

stream fishes (but see Smale and Rabeni 1995 and Beitinger et al. 2000) making it difficult to predict future changes to fish assemblages.

Groundwater interactions have a direct influence on lotic thermal regimes, which in turn influences fish distributions. The recharge rate of aquifers is declining due to increased groundwater pumping leading to reductions in spring-flow volume in many streams (Fitzhugh and Richter 2004). This reduction in recharge rate could reduce the buffering capacity of spring-fed streams making them more susceptible to climate change (Caissie 2006). In fact, remnant pools of drying streams in the Great Plains during summer are maintained via groundwater interactions and decoupling these interactions could eliminate key habitat for the Arkansas Darter *Etheostoma cragini* and other springfed obligates (Labbe and Fausch 2000). In Yorkshire, UK, groundwater pumping in the alluvial aquifer increased the diel fluctuation and mean temperature of the Yorkshire River (Cowx 2000). Streams with appreciable groundwater influence have a buffered thermal regime, allowing for cooler temperatures in the summer and warmer temperatures in the winter (Brown et al. 2005). Peterson and Rabeni (1996) found that many stream fishes (Smallmouth Bass *Micropterus dolomieu*, Longear Sunfish *Lepomis megalotis*, Shadow Bass *Amploblites ariommus*, and Black Redhorse *Moxostoma duquesnei*) in the Missouri Ozarks moved to spring-fed reaches over winter when groundwater temperatures were warmer than stream temperatures (Poole and Berman 2001). At the most basic level, the thermal regime influences fish distributions because fish are unable to survive in streams that exceed their thermal tolerances (Waco and Taylor 2010). Fish adapt to their local physicochemical conditions, which is why their

thermal tolerances could vary geographically (Strange et al. 2002). Thermal alterations could result in multiple direct and indirect consequences to the associated biota.

Critical Thermal Maxima (CTM) is the most common method for determining the maximum temperature tolerances of fishes, but it has some limitations. Standard CTM studies increase temperature at a fast rate (1°C per min – 1°C per h, Becker 1979) to prevent acclimation of fishes to the increasing temperature and continues to increase until the fish reaches critical endpoints (i.e. loss of equilibrium, operculum spasms, or death; Lutterschmidt and Hutchinson 1997). Naturally, the heating rate of streams is much slower than the rate of increase associated with CTM studies. Further, streams have diel temperature fluctuations (i.e., increased temperature during the day and decreased temperature at night) that could provide thermal refugia or reprieves allowing fishes to have greater thermal tolerances than predicted through CTM (Feldmeth and Stone 1973). Diel refuges may also allow fish to survive at higher temperatures (Hubbs 1964) or at least benefit bioenergetically (Thomas et al. 1986; Whitledge et al. 2006). A temperature tolerance study mimicking the thermal regime of streams that has both a slower rate of temperature increase and a diel period could simulate a more realistic physiological response to increasing temperatures (Becker 1979; Wehrly et al. 2007). Comparing the results of a standard CTM with the results of a longer-term temperature tolerance study could better depict how species will respond to increasing temperatures.

The objective of this study was to examine the critical response of riverine fishes to both a standard CTM and a longer-term thermal tolerance experiment. The general approach was to mimic diel changes in temperatures associated with spring fed and non-spring fed streams while integrating a CTM component. My hypotheses were that 1)

fishes exposed to a slower thermal increase would be able to acclimate to the increasing temperature and survive at higher temperatures than were determined from a more traditional CTM; and 2) that fishes exposed to a thermal regime mimicking non spring-fed streams (greater temperature fluctuations) would have a higher thermal tolerance than fishes exposed to a thermal regime mimicking spring-fed systems.

STUDY AREA

Fishes were collected from spring-fed streams of the Arbuckle Mountains ecoregion of Oklahoma (Figure 1). Many streams in the region are perennial due to spring inflows from the Arbuckle-Simpson aquifer. The Arbuckle-Simpson aquifer is 1280 km^2 and comprises dolomite, limestone and sandstone lithologies (Rahi and Halihan 2013). The aquifer is recharged primarily through precipitation and losing reaches of spring-fed streams (Savoca and Bergman 1994). The primary landscape disturbances are groundwater pumping, fracking, waste-water injection, and mining (Fairchild et al. 1990). The aquifer is isothermic, maintaining a constant temperature of approximately 18°C (Swinea 2012). Spring-fed streams of the Arbuckle Mountains have an average summer temperature of 26.1°C, a maximum temperature of 31.6°C and a range of diel shifts in temperature (i.e., average minimum and maximum temperature from June and July) of 24.3 – 28.8°C (U.S. Geological Survey, stream gage). Alternatively, non-spring fed streams have an average summer temperature of 28.2°C, a maximum temperature of 37°C and a range of diel shifts in temperature (i.e., average minimum and maximum temperature from June and July) of 25.6 – 31.5°C (U.S. Geological Survey, stream gage).

METHODS

Fish collection and acclimation. Fishes were collected in spring, summer, and autumn 2013 – 2015. Fishes were sampled with a 2.4 m seine with 0.32 cm diameter mesh that was pre-soaked in VidaLife (Western Chemical Inc., Ferndale) to minimize abrasions. Fish were transported in stream water with 5.0 g/L of uniodized salt, to reduce stress and disease (Swann and Fitzgerald 1992). In the laboratory, fish were acclimated to 20°C for at least two weeks with a 12-h light: 12-h dark photoperiod. Air stones were added to all aquaria to maintain dissolved oxygen > 6 mg/L. During acclimation, fish were fed flakes (Wardley Advanced Nutrition Perfect Protein Tropical Fish Flake Food, Secaucus) and bloodworms (Fish Gum Drops Floating Fish Food Bloodworms, San Francisco) once daily until satiation. Water quality (i.e., pH, ammonia, chloramine) was checked daily to maintain adequate conditions.

Critical Thermal Maxima (CTM). A sump system (Figure 2) with eight acrylic aquariums was used to test the thermal tolerances of fishes using a 5000-watt Smartone heater (OEM Heaters, Saint Paul, MN) as the heating source. Acrylic aquariums were used because they are better able to hold heat when compared to glass. Fishes were transferred to test aquaria with one fish in each tank and held at 20°C (i.e., average temperature of Arbuckle Mountain streams during spring-summer interface) for 24 h prior to testing. Food was suspended 48 h prior to testing. Air stones were added to maintain dissolved oxygen above 6 mg/L. Eight individuals of 15 different species representing five families were randomly selected and tested in each trial (Table 1). Water temperature was increased 2°C per h until the fish experienced loss of equilibrium and death as the endpoint (Lutterschmidt and Hutchison 1997b). A survival control was completed for all

15 species with 10 replicates. Control fish were held in the eight aquariums fed by the sump system at 20°C for 24 h.

Longer-term temperature tolerance. Sump systems (Figure 2) with five acrylic aquariums were used to test a longer-term maximum tolerance using 1700-watt Smartone heaters (OEM Heaters, Saint Paul, MN) as the heating source. Fish were transferred to testing aquaria 24 h prior to testing and held at 20°C. Air stones were added to sump systems to maintain dissolved oxygen > 6 mg/L. Fish were fed bloodworms (Fish Gum Drops Floating Fish Food Bloodworms, San Francisco) once daily until satiated. Five individuals of 10 species representing four families were randomly selected for each trial (Table 1). The temperature regime of trial one mimicked a typical spring-fed stream during June and July in the Arbuckle Mountains (U.S. Geological Survey, stream gage 07332390 Blue River near Connerville, OK), and increased 4°C each day and decreased 3°C each night, having an overall increase of 1°C each day. The temperature regime of trial two mimicked a typical non spring-fed stream in the Arbuckle Mountains (U.S. Geological Survey, stream gage 07330700 Caddo Creek Site 7cmp near Gene Autry, OK), and increased 8°C each day and decreased 7°C each night, having an overall increase of 1°C each day. The SF and NSF trials are hereafter referred to as acclimation periods because the SF group had a longer amount of time to acclimate to the increasing temperatures. The temperature in both treatments continued to increase until each individual reached the endpoint of death. A survival control for each treatment was completed for each species with 10 replications. The thermal regime of the control fluctuated from 20°C to 25°C each day for two weeks.

Data analyses. All temperature tolerance data were normally distributed and analyzed using linear models. The CTM loss of equilibrium (CTM LOE) and death (CTM D) endpoints were analyzed using a general linear mixed model (GLMM) with a one-way treatment structure with 15 levels (species) and was blocked by sump system. Longer-term temperature data (with two acclimation periods representing SF and NSF systems) and the CTM D data were analyzed using a general linear model (GLM) with a one-way treatment structure with 10 levels (species). I used the endpoint of D rather than LOE because fish behavioral responses to longer-term temperature increases were not the same as CTM; fish did not experience LOE response associated with CTM. A Tukey-Kramer post hoc test adjusted for multiple comparisons was used to determine where significant differences occurred if the overall models were significant. The CTM and both treatments (SF and NSF) in the longer-term temperature tolerance were replicated 10 times for each species. Significance was determined at $\alpha \leq 0.05$. All analyses were performed in SAS version 9.4 (SAS Institute Inc. 2013).

RESULTS

Traditional CTM

The general linear mixed model comparing the CTM LOE and CTM D of 15 species was significant for the main effects of species ($F_{14, 259} = 30.25$, $P \leq 0.01$) and endpoint (D or LOE, $F_{1, 249} = 18.32$, $P \leq 0.01$), but the interaction between species and endpoint was not significant ($F_{14, 249} = 0.8$, $P = 0.67$). Species with the highest CTM were mid-channel minnows and sunfish, whereas species with the lowest CTM were spring-fed obligates, Oklahoma species of greatest concern and benthic darters and minnows (Figure 2). The

species that had the highest CTM were (see Appendix A for specific values of individual CTM LOE and CTM D): Bluntnose Minnow *Pimephales notatus,* juvenile Bluegill *Lepomis macrochirus* and Blacktail Shiner *Cyprinella venusta*. All three species had a maximum thermal tolerance of 36°C. The species with the lowest CTM (34.5°C) were: Redspot Chub *Nocomis asper* (Oklahoma greatest concern), Central Stoneroller *Campostoma anomalum*, Orangebelly Darter *Etheostoma radiosum* (Oklahoma greatest concern), Least Darter *Etheostoma microperca* (Oklahoma greatest concern), Logperch *Percina caprodes* and Orangethroat Darter *Etheostoma spectabile*. The average CTM of all species was statistically lower for the endpoint LOE (34.9°C) compared to the endpoint D (35.2°C).

Longer-term thermal tolerances

The longer-term tolerance data were analyzed using a general linear model comparing the CTM D for both SF and NSF trials. The main effects of species ($F_{9, 231} = 79.45$, $P \leq 0.01$) and acclimation period ($F_{2, 11} = 32.3$, $P \leq 0.01$) were significant. More importantly, the interaction between species and acclimation period was significant ($F_{18, 231} = 5.7$, $P \leq 0.01$) suggesting the species' thermal tolerances differed depending on the length of the acclimation period (CTM D, SF or NSF).

Species differences within acclimation periods. Results from the Tukey-Kramer post hoc test indicated there were several differences in the thermal tolerances within the two acclimation periods (SF and NSF, Figure 3). Juvenile Bluegill had the highest temperature tolerance for both SF and NSF trials. The species that had the lowest temperature tolerance for both SF and NSF trials were spring-fed obligates and benthic

darters. The species with the lowest temperature tolerances were (see Appendix B for specific values of individual SF and NSF): Logperch, Southern Redbelly Dace *Phoxinus erythrogaster*, Orangebelly Darter, and Orangethroat Darter. Redspot Chub, a spring-fed obligate, had a significantly lower thermal tolerance in the SF acclimation period but not in the NSF acclimation period (Figure 3). For both acclimation periods (SF and NSF), fishes that had the highest thermal tolerances were either mid-channel minnows or sunfish, whereas species with the lowest thermal tolerances were benthic species, spring-fed obligates, or Oklahoma species of greatest concern (Redspot Chub and Orangebelly Darter).

Species differences between acclimation periods. Many species were able to acclimate to slower heating in the SF group and survive at higher temperatures (Figure 4). The thermal tolerances of all species significantly differed between the traditional CTM D and NSF. Seventy percent (7 of 10) of the species had a thermal tolerance approximately 2°C higher in the SF compared to the CTM D, except for Southern Redbelly Dace, Orangebelly Darter, and Orangethroat Darter. Forty percent (4 of 10) of species had significantly higher thermal tolerances in the NSF acclimation period compared to the SF: Redspot Chub, Brook Silverside, Orangebelly Darter, and Southern Redbelly Dace.

DISCUSSION

The results of this study are, to my knowledge, the first to show that longer-term temperature tolerance studies allow fishes to acclimate and survive at higher temperatures compared to traditional CTM studies. Traditional CTM studies were developed to be slow enough to prevent core temperatures of fish from lagging behind water temperature

but fast enough to prevent fish from acclimating to the increasing temperature (Beitinger et al. 2000). The fast temperature increase of CTM studies was thought to allow biologists to determine species physiological response to temperature but not their ecological response to increasing stream temperature, such as would occur due to pulse disturbances (i.e., isolated in a drying pool) (Ostrand and Wilde 2001). Many ecologists agree that CTM methods are not realistic of natural conditions and ignore complex environmental conditions; however, CTM studies are still useful for ranking the sensitivity or tolerance of different species (Smale and Rabeni 1995). Longer-term temperature tolerance studies provide insight on species response to increases in temperature due to landscape or climate changes (i.e., press disturbance). The first longer-term temperature study was completed by Hickman and Dewey (1973) on Duskystripe Shiner *Notropis pilsbryi* and Bluegill where water temperature increased at a constant rate (i.e., no diel fluctuation) of 2°C per day until fish died. The method was later defined as chronic lethal method (CLM) and results suggested temperature tolerances defined using CLM were lower than CTM (Beitinger 2000). The development of longer-term temperature tolerance studies with diel fluctuations is novel and has only been used recently to assess changes in catfish growth (Stewart et al. 2015). Combining traditional CTM with longer-term temperature studies allows for improved predictions of species acclimation abilities and fish-assemblage changes.

Thermal tolerances of the species used in this study reflect their stream habitat-use patterns. The thermal tolerance of all benthic species and spring-fed obligates were lower than all mid-channel and surface species. Benthic regions maintain cooler, stable thermal regimes (Brown et al. 2005; Schmidt et al. 2006; Seilheimer and Fisher 2010)

compared to surface water that has wider diel-temperature fluctuations due to solar radiation (Webb and Zhang 1999; Caissie 2006). Species often disperse among stream reaches to seek optimal temperatures (Todd and Rabeni 1989; Peterson and Rabeni 1996), but few studies have determined if fishes select fine-scale habitats that provide optimal temperatures (but see Brewer 2013). Furthermore, habitat use by fishes has mostly focused on the horizontal features of the stream such as channel units (i.e., riffle, run, pool) (Bart 1989; Peterson and Rabeni 2001), but the importance of vertical upwelling from groundwater can also influence habitat use (Brewer 2013). My results could also apply at a landscape scale where species in headwaters with higher thermal tolerances experience greater environmental fluctuations than downstream (Ostrand and Wilde 2001). Comparing the thermal tolerances of all species and acclimation periods provides a predictive tool for identifying species and guilds that are more susceptible to temperature perturbations; however, comparing species thermal tolerances between acclimation periods also provides insight on the acclimation potential of different species.

The thermal tolerance of fishes could be influenced by the thermal regime they occupy (i.e., wide temperature fluctuations, stable temperatures). All 10 species in my study had, on average, higher temperature tolerances in the NSF compared to the SF trials (four species with significantly higher tolerances). This shows that fishes can survive at warmer temperatures than predicted by CTM by acclimating to the wider thermal fluctuations but that some species might be more plastic than others. For example, Orangethroat Darters had higher CTM when sampled from rivers with greater temperature fluctuations, whereas individuals from more constant regimes (i.e., spring-fed) had lower CTM (Faminella and Matthews 1989). However, pupfish *Cyprinodon*

collected from fluctuating and stable temperature environments had the same acclimation ability and thermal tolerance (Brown and Feldmeth 1971). Levins (1969) hypothesized that species that historically occupied dynamic streams but then transitioned to streams with more stable thermal regimes would be less plastic than other species. Additionally, adaptive changes to the phenotypic plastic responses of some fishes has been observed, such as populations of grayling (*Thymallus thymallus*), isolated for over 15 years have adapted to different thermal regimes, preferring and growing optimally at different temperatures (Crozier and Hutchings 2013). Although all of the species in my study were collected from spring-fed streams with limited temperature fluctuations, my results showed that species' thermal tolerances still varied based on the thermal exposure.

Understanding thermal acclimation is important for predicting the sensitivity of long-term temperature changes, such as climate, but can be difficult to study because of length of studies, and differences among species. All of the surface and mid-channel species were able to acclimate and increase their thermal tolerances from the CTM to the longer-term acclimation period by 3 – 6°C, whereas benthic and spring-fed obligates only increased their thermal tolerance by 1 – 3°C. However, Sorte et al. (2011) compared the short-term thermal tolerances of mussels, tunicates, and bryozoans across the U.S. and determined species with the highest temperature tolerances were most susceptible to stream temperature increases. The authors also concluded that species with the lowest thermal tolerances had the most geographic variability in tolerances. Acclimation ability is complex and varies by species. Although my results showed which species are more susceptible to temperature increases and provided insight on their acclimation ability, it is difficult to compare even longer-term trials with evolutionary timelines. More research is

needed to better understand the acclimation ability and thermal tolerance of fishes under varying climate-change scenarios.

Fish-assemblage changes could be more accurately predicted by modeling stream temperatures at more fine spatial scales. Many temperature models are applicable to questions at the reach (e.g., Johnson 2004; Davis et al. 2015) or more coarse scales (e.g., Somers et al. 2013; Macedo et al. 2015). Temperatures of spring-fed streams can vary significantly across microhabitats (Clark et al. 1999; Brewer 2013) but modeling temperature at this scale is rare. More fine-scale modeling would be helpful to our understanding of fish refuges that may allow persistence of fishes during drought and other harsh periods (Nielsen and Lisle 1994; Caissie 2006). More importantly, refuge locations could be protected by preventing water withdrawals from the alluvial aquifer during certain time periods. For example, groundwater pumping can increase summer stream temperature at the reach level by 0.5°C or by 2.5 – 3.25°C if associated with an upstream dam (Risley et al. 2010). Finer-scale models that incorporate spatial and temporal thermal heterogeneity could allow better predictions of which fish guilds are more susceptible to climate change. My temperature tolerance studies show different patterns when a diel refuge was included, patch refuges could allow species to persist in a reach that has, on average, high temperatures over the period of interest. Patch refuges for some physicochemical constituents (e.g., dissolved oxygen) have been studied in lake and reservoir environments where species made migrations to different patches to avoid harsh or deadly conditions (Magnuson et al. 1985). Incorporating patch refuges and stream spatial heterogeneity into fine-scale temperature models will improve predictions on future fish assemblage changes.

Coarse-scale temperature models are useful, however, for showing conservative patterns of fish distributions and providing some information on basic thermal tolerances. Recently, many coarse-scale models were developed to show global and continental stream temperature changes related to climate change (Eaton and Scheller 1996; Xenoploulos et al. 2005; Van Vliet et al. 2013). Eaton and Scheller (1996) analyzed the potential effects of climate change on stream thermal habitats within the U.S. and determined that optimal thermal habitats for cold, cool-water and warmwater fishes would decline by 50% and by 14.2%, respectively. Wehrly and Wiley (2003) modeled average and diel stream temperature regimes along with fish distributions in Michigan to develop a thermal classification system for rivers and fishes (coldwater, cool-water, warmwater). Results from the classification system predicted the ecological integrity of the river and fish groups based on stream structure, landscape alterations, and species richness. More studies are needed to determine the influence of landscape alteration and climate change on structurally different streams (i.e., spring fed, non spring fed). The thermal regime of spring-fed and non spring-fed streams is influenced differently by atmospheric temperature and landscape characteristics, so varying levels of alteration could change the thermal regimes of rivers in drastically different ways. Incorporating the results of fine and coarse-scale models into temperature-tolerance studies could improve our understanding on the influence that future landscape alterations and climate scenarios could have on fish assemblages.

Table 1. Mean length (range) of fish species used in critical thermal maximum (CTM), spring fed (SF) and non spring fed (NSF) trials.

Common name	Scientific name	CTM mean length (range) (mm)	SF mean length (range) (mm)	NSF mean length (range) (mm)
Orangethroat Darter	*Etheostoma spectiabile*	48 (46–56)	50 (46–55)	49 (42–57)
Orangebelly Darter	*Etheostoma radiosum*	69 (54–86)	57 (50–59)	60 (50–65)
Least Darter	*Etheostoma microperca*	34 (31–37)		
Logperch	*Percina caprodes*	95 (76–125)	97 (80–110)	90 (80–100)
Brook Silverside	*Labidesthes sicculus*	62 (54–74)	61 (54–65)	64 (53–70)
Bluntnose Minnow	*Pimephales notatus*	54 (45–60)	58 (51–65)	56 (50–65)
Bigeye Shiner	*Notropis boops*	63 (54–70)		
Striped Shiner	*Luxilus chrysocephalus*	93 (57–139)		
Central Stoneroller	*Campostoma anomalum*	82 (63–83)	75 (63–97)	75 (60–80)
Redfin Shiner		61 (50–68)		
Blacktail Shiner	*Cyprinella venusta*	75 (65–90)	70 (54–78)	69 (60–80)
Southern Redbelly Dace	*Phoxinus erythrogaster*	65 (52–86)	52 (47–57)	54 (42–63)
Redspot Chub	*Nocomis asper*	119 (102–146)	83 (70–115)	73 (55–96)
Bluegill	*Lepomis macrochirus*	66 (55–80)	58 (56–60)	53 (45–67)
Golden Redhorse	*Moxostoma erythrurum*	84 (75–92)		

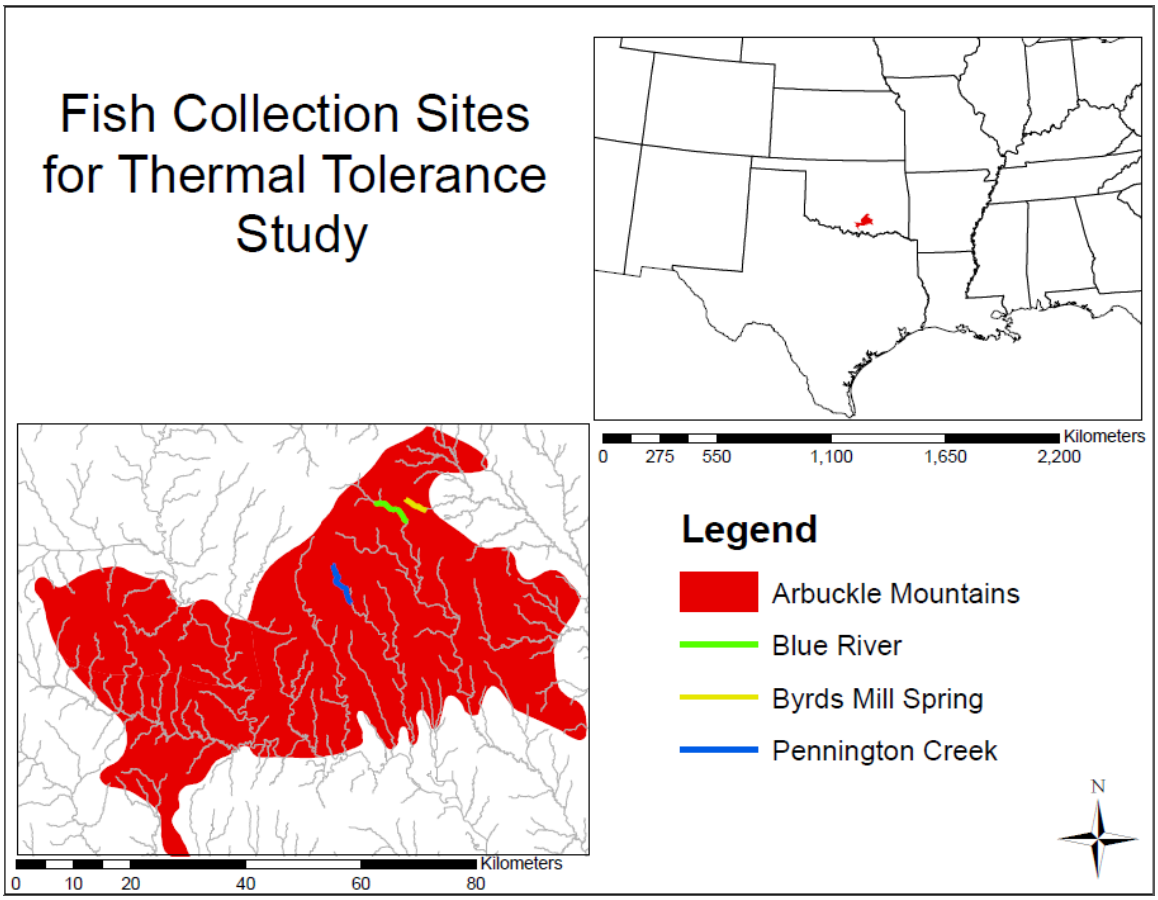

Figure 1. Fishes for the critical thermal maxima and longer-term temperature tolerance study were collected at Blue River, Pennington Creek, and Byrds Mill Spring in the Arbuckle Mountains, Oklahoma, USA.

Figure 2. Experimental sump system used to determine critical thermal maxima and longer-term temperature tolerance of fishes from the Arbuckle Mountain ecoregion.

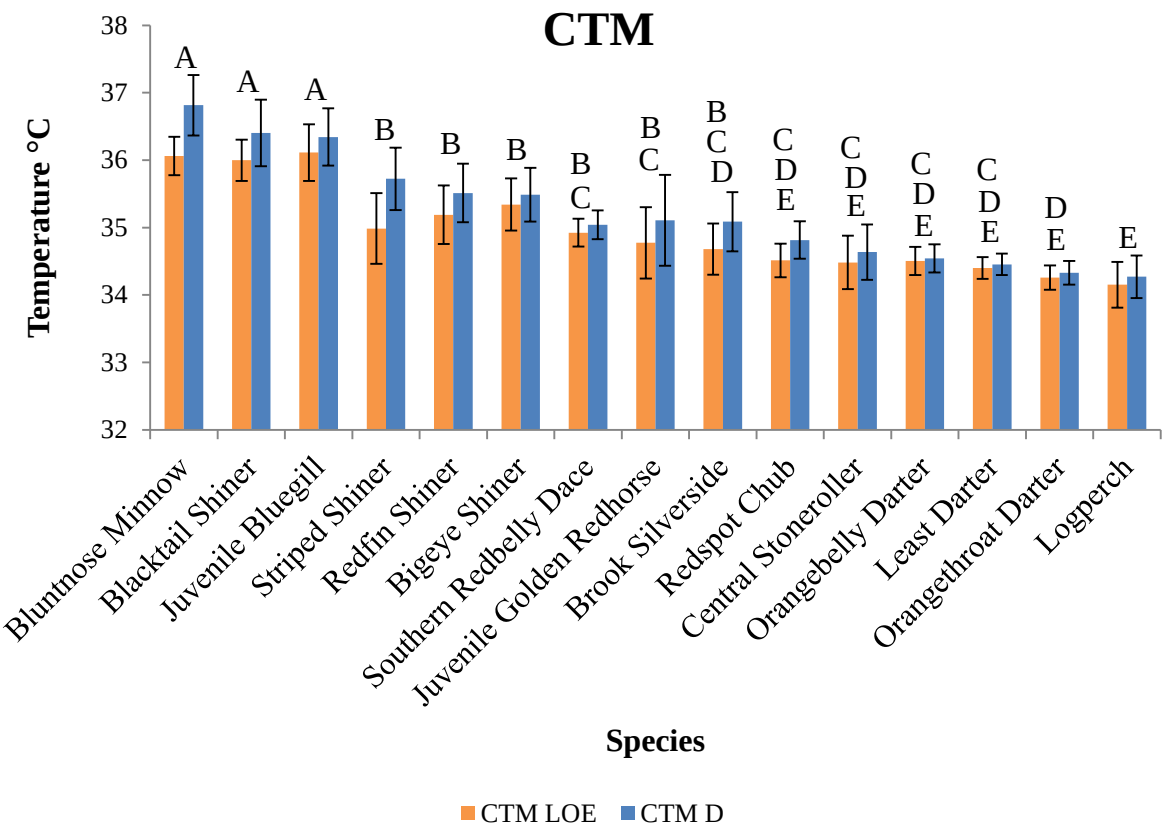

Figure 2. Critical thermal maximum (CTM) for endpoints loss of equilibrium (LOE) and death (D) for 15 Arbuckle Mountain stream fishes. There were no significant differences between the two endpoints for each species. Species with same letters indicate statistically equivalent species in CTM from Tukey-Kramer post-hoc test adjusted for multiple comparisons.

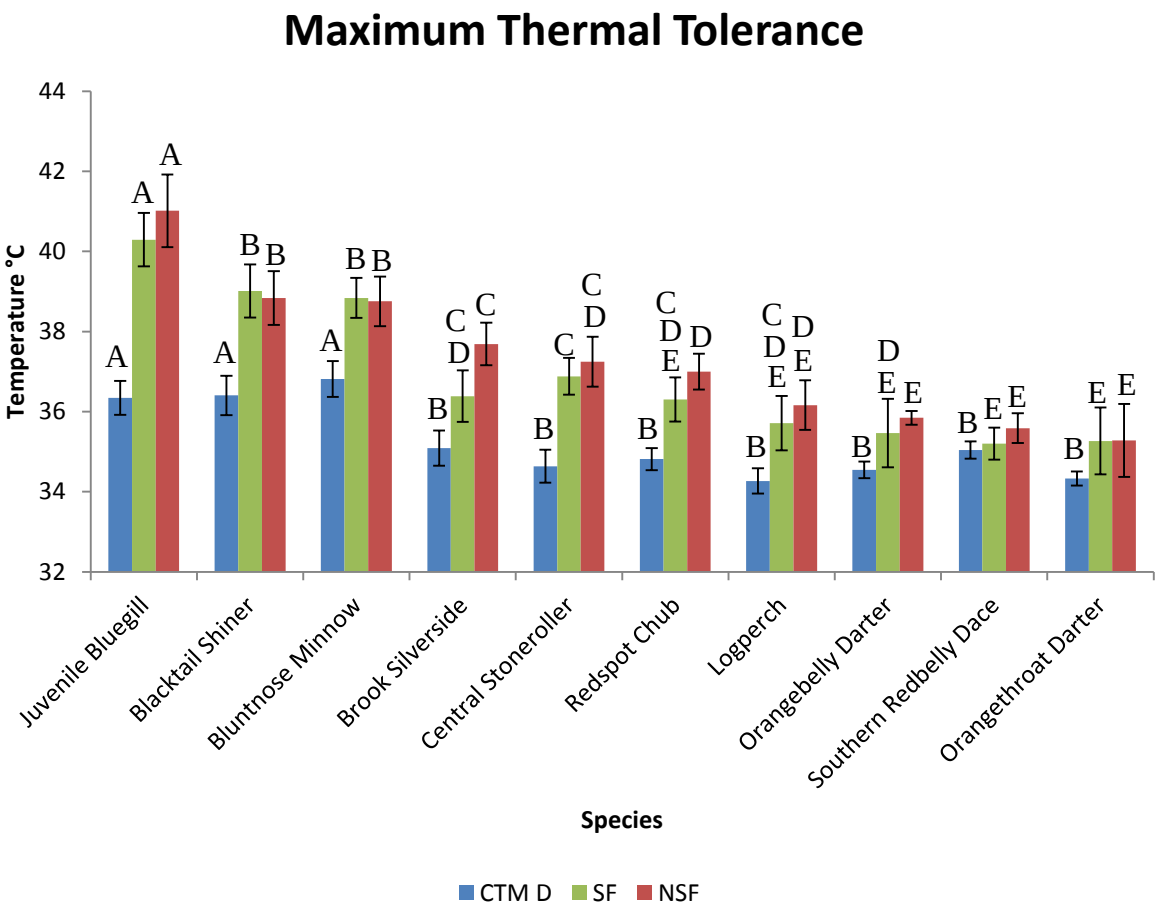

Figure 3. Mean thermal tolerance of fishes from Arbuckle Mountains for three acclimation periods: critical thermal maximum death (CTM D), spring fed (SF) and non spring fed (NSF). Species with same letters indicate statistically equivalent species in each acclimation period from Tukey-Kramer post-hoc test adjusted for multiple comparisons.

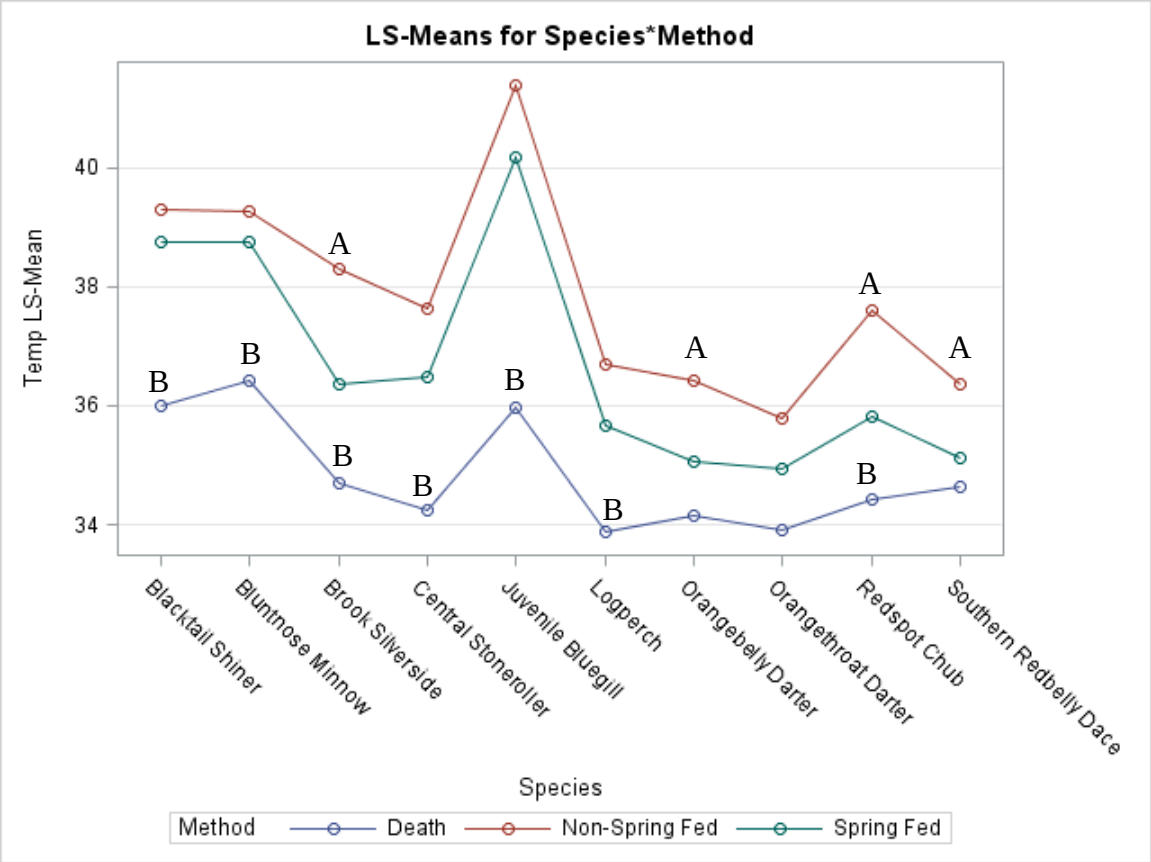

Figure 4. Nodes represent mean thermal tolerance of fishes from the Arbuckle Mountains for three acclimation periods: critical thermal maximum death (CTM D), spring fed (SF) and non spring fed (NSF). Letters represent statistical difference of species between the different acclimation periods. All species were statistically different between CTM D and NSF, so no letter was used to signify differences. Letter A signifies differences between NSF and SF and letter B signifies differences between SF and CTM D. Statistical differences were determined from Tukey-Kramer post-hoc test adjusted for multiple comparisons.

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APPENDICES

Appendix 1. Mean (°C), standard deviation (SD), and 95% confidence interval of critical thermal maximum (CTM) for loss of equilibrium (LOE) and death (D) endpoints.

		CTM Loss of Equilibrium			CTM Death		
Common name	Scientific name	Mean	SD	95% CI	Mean	SD	95% CI
Bluntnose Minnow	*Pimephales notatus*	36.1	0.46	±0.28	36.8	0.72	±0.45
Juvenile Bluegill	*Lepomis macrochirus*	36.1	0.68	±0.42	36.3	0.68	±0.42
Blacktail Shiner	*Cyprinella venusta*	36.0	0.49	±0.31	36.4	0.72	±0.49
Bigeye Shiner	*Notropis boops*	35.3	0.63	±0.39	35.5	0.64	±0.40
Redfin Shiner	*Lythrusus umbratilis*	35.2	0.70	±0.43	35.5	0.70	±0.44
Striped Shiner	*Luxilus chrysocephalus*	35.0	0.84	±0.52	35.7	0.75	±0.46
Southern Redbelly Dace	*Phoxinus erythrogaster*	34.9	0.33	±0.21	35.0	0.34	±0.21
Juvenile Golden Redhorse	*Moxostoma erythrurum*	34.8	0.85	±0.53	35.1	1.09	±0.67
Brook Silverside	*Labidesthes sicculus*	34.7	0.61	±0.38	35.1	0.71	±0.44
Redspot Chub	*Nocomis asper*	34.5	0.40	±0.25	34.8	0.45	±0.28
Central Stoneroller	*Campostoma anomalum*	34.5	0.61	±0.40	34.6	0.63	±0.41
Orangebelly Darter	*Etheostoma radiosum*	34.5	0.34	±0.21	34.5	0.33	±0.21
Least Darter	*Etheostoma microperca*	34.4	0.26	±0.16	34.5	0.26	±0.16
Orangethroat Darter	*Etheostoma spectiablile*	34.3	0.29	±0.18	34.3	0.29	±0.18
Logperch	*Percina caprodes*	34.2	0.55	±0.34	34.3	0.51	±0.32

Appendix 2. Mean (°C), standard deviation (SD), and 95% confidence limits of non spring fed (NSF) and spring fed (SF) longer-term temperature-tolerance study.

		Spring Fed			Non Spring Fed		
Common name	Scientific name	Mean	SD	95% CI	Mean	SD	95% CI
Juvenile Bluegill	*Lepomis macrochirus*	40.2	1.05	±0.67	41.4	1.47	±0.91
Bluntnose Minnow	*Pimephales notatus*	38.7	0.84	±0.50	39.3	1.00	±0.62
Blacktail Shiner	*Cyprinella venusta*	38.7	1.11	±0.66	39.3	1.08	±0.67
Central Stoneroller	*Campostoma anomalum*	36.5	0.65	±0.46	37.6	1.00	±0.62
Brook Silverside	*Labidesthes sicculus*	36.4	0.94	±0.65	38.3	0.86	±0.53
Redspot Chub	*Nocomis asper*	35.8	0.84	±0.55	37.6	0.72	±0.45
Logperch	*Percina caprodes*	35.7	1.14	±0.68	36.4	1.00	±0.62
Southern Redbelly Dace	*Phoxinus erythrogaster*	35.1	0.60	±0.40	36.8	0.06	±0.37
Orangebelly Darter	*Etheostoma radiosum*	35.1	1.45	±0.86	36.4	1.17	±0.17
Orangethroat Darter	*Etheostoma spectabile*	35.0	1.40	±0.84	35.8	1.47	±0.91

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